The concealed copulatory structures of the *Pyrgomorphidae*

(Orth. Acridoidea)

PART II. TRIBES *FIJIPYRGINI, VERDULIINI, BRUNNIELLINI, PSEDNURINI, MITRICEPHALINI, GELOIINI, SAGITTACRIDINI, GYMNOHIPPINI* AND *MALAGASPHENINI* [1].

BY

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ABSTRACT.

The *Pyrgmorphidae* are divisible into 30 tribes on the basis of their external morphology, phallic and concealed female structures — some change from the previous arrangement of these tribes is proposed. A linear sequence is difficult to devise because of the lack of correlation in the different tribes between 'primitive and 'derived' characters. The tribes are placed in two arbitrary groups, A and B, based largely on the form and disposition of the metasternal pits. Within Group A, four, and within Group B, six series of tribes are recognized. The present work deals in detail only with Series I and II of Group A, but all series and tribes are listed, together with notes on recent changes.

For each tribe of Series I and II, the full tribal synonymy, a definition, with particular reference to the phallic and concealed female structures, and all included genera and species with their general geographic distributions are given. The phallic and concealed female structures of a representative of each genus are illustrated in detail (except for genera in which only one sex is known). Some discussion of tribal relationships is included where appropriate.

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1 For Part I, see Kevan, Akbar and Chang. *Eos* (1969). This includes a general discussion of the structures and a glossary of terms. The authors wish to repeat their grateful ackonowledgements to those organizations and persons already referred to in Part I. Support was received from the National Research Council of Canada.

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Introduction.

As indicated by Kevan and Akbar (1964), the relationships of the various groups of *Pyrgomorphidae* to one another are very difficult to assess because primitiveness or specialization in any one morphological feature is not necessarily paralleled by comparable conditions in other characters. No living pyrgomorphid seems to represent anything close to the ancestral stock from which the others may have been derived; all genera seem to be more or less specialized (or 'derived') in several features, even although one or more characters that are believed to be comparatively primitive may be retained. This is true both for external morphology and for the structure of the concealed genitalia; and it is also true as between sexes of the same species. Further, there seems to be no division of the family into major units sharing common features that are sufficiently distinctive to permit the recognition of subfamilies.

On the other hand, most genera may be grouped together, on the basis of morphological similarities, into 30 fairly readily distinguishable tribes. As in any classification system, some of the tribes are large, or moderately so, while others comprise only a few genera. Six genera are sufficiently anomalous to require the recognition of monogeneric tribes. The first dozen tribes listed by Kevan and Akbar (1964), together with most (but not all) *Verduliini,* differ from the others in that the metasternal pits are unconnected anteriorly by a straight suture (although a curved line may be present) and are generally large, open, usually crescentic and close together (or even contiguous) — see Kevan and Akbar *(l. c.,* pp. 1513-14, couplet 5). The difference is, however, too small, insufficiently reliable in a few cases, unaccompanied by other common characters and of too dubious phylogenetic significance to enable one to recognize two subfamilies. The form of the metasternal pits is probably, to a large extent, only a manifestation of general body form. Similarities in phallic structures and other characters may cut across the two groups. For convenience, however, we here recognize those forms with approximated, open metasternal pits as Group A (having the *Orthacridini* as its largest component) and the remainder as Group B (in which the *Pyrgomorphini* have the most numerous genera). The closest phylogenetic relationships, however, do not always seem to be within the respective groups to which the

different tribes are assigned. Thus *Orthacridini* (Group A) and *Chlorizeinini* (Group B) are often generally similar in appearance and may even have certain genitalic characters in common. Similary, the *Nereniini* (Group A) and *Desmopterini* (Group B) have several such common characters (they may even be related), although they are vastly different from one another in outward appearance. The converse may also be true; genera that appear to belong to the same tribe may be incorrectly assigned.

It is impossible to place together all those tribes in which some genera, at least, possess what may be regarded as 'primitive' characters, because many of them are clearly not closely related when other features are considered. Thus *Tagastini* have divided aedeagal sclerites (regarded as being primitive) but they do not appear to have a close affinity with other tribes possessing this character. Some tribes may have a well developed spermathecal appendage (regarded as being primitive), but are highly specialized in other characters (e. g. *Nereniini);* some members of a tribe may possess a spermathecal appendage, and others may not (e. g. *Desmopterini, Sphenariini).* One cannot, therefore, for the most part, construct a satisfactory dendrogram indicating relationships, nor can one present any other meaningful type of phylogenetic diagram, even in three dimensions, though numerical methods may help.

Nevertheless, in order to treat the various tribes, a linear sequence is demanded. One must, as it were, endeavour to arrange logically, as on a ladder, the cross-section of the top of a bush the lower parts of whose branches are invisible! All that may be done, therefore, is to present a largely arbitrary arrangement of tribal 'Series' within Groups A and B. Kevan and Akbar (1964) have already attempted this, recognizing five such series, of which the first included all those tribes here placed in Group A, except for the *Verduliini* (at the beginning of their second series) and *Fijipyrgini* (erected subsequently by Kevan (1966 c)). Here we subdivide the original Series I into four and make certain other subdivisions, rearrangements in the sequence and minor modifications. The arrangement here adopted for Group A is as follows:

Series I: Fijipyrgini, Verduliini [to which have been added *Spinacris* and *Meubelia* (Kevan, 1966 b)], *Brunniellini, Psednurini, Mitricephalini* [*Kuantania* is here removed to *Orthacridini*[4]]; *Series II: Ge-*

[4] The key to tribes and subtribes given by Kevan and Akbar (1964) must be

loiini [*s. str.* = *Pseudogeloiini* of Kevan and Abkar (1964) — see Descamps and Wintrebert (1966) — i. e. *Geloius, s. str.*, and *Pseudogeloius*], *Sagittacridini* [= *Geloiini, sensu* Kevan and Akbar (1964) and previous authors, and without *Uhagonia* — see next], *Gymnohippini* [*Uhagonia,* formerly listed in what is now *Sagittacridini,* added — see Kevan (1966 c and 1968 a)], *Malagasphenini; Series III: Chapmanacridini, Ichthiacridini, Ichthyotettigini, Orthacridini* [*Colemania, Ramakrishnaia, Nilgiracris* and *Popoviina (Popovia* and *Parortacris)* removed to next tribe; *Pseudorubellia* removed to *Chlorizeinini* (Group B); *Kuantania* transferred to *Orthacridina* (see above) and the recently described *Acropyrgus* now added to *Caprorhinina* (Kevan, 1968 a)], *Popoviini*[5]*; Series IV: Nereniini* [to which have been added *Megra, Kapaoria, Fusiacris, Tarbaleopsis, Buergersius, Paratarbaleus, Noonacris* and *Oxytarbaleus* (see Kevan, 1966 e)].

The following Series constitute Group B:

Series V: Desmopterini [subgenus *Brachydesmoptera* of the genus *Apodesmoptera* has recently been added by Kevan (1966 f); subgenus *Desmopterula* of *Desmoptera* has fallen as a synonym of *Platydesmoptera* (see Kevan, 1966 c, f)], *Monistriini; Series VI: Chlorizeinini* to which should be added the two genera *Feacris* (see Kevan, 1969) and *Pseudorubellia* (removed from *Orthacridini* to subtribe *Humpatellina*)], *Poekilocerini, Phymateini; Series VII: Schulthessiini* [*new status* — no longer regarded as a subtribe of *Atractomorphini*], *Taphronotini, Dictyophorini; Series VIII: Tagastini, Pseudomorphacridini, Atractomorphini* [including subtribe *Occidentosphenina, new status,* which has common genitalic features, both male and female, with the *Atractomorphina,* notably an anchor-shaped epiphallus and a bifid spermatheca]; *Series IX: Sphenariini* [including subtribe *Rubelliina, new status,* and *Sphenexiina (Rubellia* and *Sphenexia* are here reunited with this tribe —the latter now removed from *Pyrgomorphini*— on the basis

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altered as follows: p. 1514, first part of couplet 8 to exclude micropterous and apterous forms; second part to include species without a median ocellus.

[5] *New status:* given full tribal recognition on the basis of the phallic structures, notably the broad, rounded cingulum, the large, wide zygoma and the absence of anterior ventral processes on the apodemal plates; other differences will be noted later. The Indian genera *Colemania, Ramakrishnaia* and *Nilgiracris* form a *new subtrile, Colemaniina,* which may be distinguished externally from *Orthacridina* — where they were placed by Kevan and Akbar (1964) — and from *Popoviina, s. str.*, by their more fusiform shape, and by the characters given by Singh and Kevan (1965) and by Kevan and Akbar *(l. c.)* respectively.

of such features as the similarity of the epiphallus, spermatophore sac and spermatheca to those of the *Sphenariina (Prosphena)* and of the form of the cingulum to that of the *Mekongianina (Yunnanites); Mekongiella* has been added to the latter subtribe (see Kevan, 1966 g)], *Omurini; Series X: Chrotogonini* [*Moxicus now = Caconda*], *Pyrgomorphini* [*Punctisphena* moved from subtribe *Parasphenina* to *Pyrgomorphina* and the recently described genus *Carinisphena* placed with it (Kevan, 1966 d), *Sphenexiina* have been transferred to *Sphenariini* (see above); *Arbuscula* and *Geloiodes* remain anomalous and they should probably be excluded from the subtribe *Pyrgomorphina*].

Although there have been additions and considerable rearrangement of tribes, as noted above, it would not appear necessary at this time to present a new key to the tribes of *Pyrgomorphidae,* since that given by Kevan and Akbar (1964), but incorporating the modifications of Kevan (1966 b-e) and in Footnotes 4 and 5, is still valid. It may be noted, however, that, in Couplet 5, *Pseudorubellia* (now *Chlorizeinini)* falls into the second part leading to Couplet 13, and thus presents less difficulty than formerly.

In the difficult task of arranging tribes and genera in a linear sequence, certain guiding principles have been followed wherever possible. Some of these principles, however, may not be well founded. Within each series, those forms having some more obvious supposedly primitive character have been listed first — although occasionally some manoeuvering has occurred in order to place forms with related zoogeographical distributions or similar morphological features together. Unfortunately the mixture of so-called primitive and derived or specialized characters in any given tribe or genus has made difficult adherence to such principles as there are. Characters regarded as being more primitive are, *in external morphology:* fully or reasonably well developed tegmina and hind wing; hind wings brightly coloured and with dark margins or apices; the dorsal basal lobe of the hind femur projecting as far or further forward than the ventral lobe; metasternal pits open and near together (very dubiously primitive); fastigium of vertex short or of moderate length; *in the phallic structures:* separate apical aedeagal sclerites, or with the apices of the aedeagal sclerites constricted or 'forked'; denticulation of aedeagal valves; endophallic apodemes with ventral processes; valves of cingulum complex or denticulate or both; central membrane of ectophallus extensive; apodemal plates of cingulum pointed anteriorly in lateral view or with ventral processes; ectophallic

membrane sclerotized to form a 'hood' (possibly not primitive); the general from of the ectophallus more complex (possibly due to specialization and not primitive); epiphallus of the general characteristic form for the family, allowing that large, anterior processes and large appendices may indicate the more primitive types (it may, however, be that variability, indicating plasticity of form of the epiphallus, is indicative of a more primitive condition); in *female characters:* variable forms of columella-like structures (great reduction or absence of these structures probably indicates a derived condition); ornamentation of post-vaginal sclerite (striae, denticulation, etc.); presence of a spermathecal appendage, particularly when this is clearly situated on the main spermathecal duct; a large, well demarcated spermathecal caecum. It would also seem that a "Gondwanian" (Indo-Malayan, Australasian, Madagascan) distribution is most ancient.

It cannot be sufficiently emphasized that it is seldom that more than one or two so-called 'primitive' characters are coincident. Different tribes may retain different 'primitive' characters — such as separate apical aedeagal sclerites or a basically bifid receptaculum seminis — while exhibiting a high degree of specialization — such as apterism or complex cerci or epiphallus — in others. Most tribes are reasonably easy to recognize by means of a combination of external and concealed morphological characters (even if this sometimes amounts to no more than lack of noteworthy special features), but phylogenetic relationships between tribes are evident only in a few instances.

Group A.

Metasternal pits usually large, open and close together, not connected anteriorly by a straight suture (except sometimes in *Verduliini).* [In certain robust females *(Gymnohippini)* the metasternal pits may be widely separated and connected by a rather straight suture, but this does not join the *anterior* extremities of the pits]. Body form generally cylindrical or elongate, not commonly strongly fusiform; fastigium of vertex often (but by no means usually) short and blunt. Hind femora often having the dorsal and ventral basal lobes subequally produced or the dorsal lobe the more prominent (as in most *Acridoidea).* This feature is not found in Group B. Predominantly 'Gondwanian' in

distribution; absent from the Palaearctic region and from South America although occurring in Mexico; poorly represented on the African continent.

SERIES I.

This is a miscellaneous assemblage of anomalous tribes, occuring in the Indo-Malayan and South Pacific regions, which show some tenuous relationships to each other. Except for the genus *Megra,* it includes all the macropterous and reasonably fully alate species of Group A, only some *Verduliini* and normal *Psednurini* being micropterous or *(Psednura)* apterous. All *Pyrgomorphidae* in which the galeae of the maxillae turn forward over the labrum (merely an adaptation to graminivorous feeding and of little phylogenetic significance) are included here. *Psednurini* may be distinguished from all other *Pyrgomorphidae* in having this character particularly pronounced, and in their bacilliform shape. *Verduliini* are readily recognizable by their very large, elongate, denticulate aedeagal valves, large ventrolateral valves of the cingulum, very large, deep basal emargination of the cingulum and peculiarly ornamented post-vaginal sclerite. *Megra,* the only fully winged member of Group A not in this series, is excluded because its phallic and concealed female structures (combining a very extensive central membrane of the ectophallus, strongly inflected dorsal inflections of the endophallic apodemes, a transversely striated spermatophore sac and a long, greatly coiled receptaculum seminis) place it in the *Nereniini* (Series IV).

TRIBE 1. FIJIPYRGINI.
(Fig. 1).

Tribe *Fijipyrgini* Kevan, 1966, *Pacif. Ins.,* VIII, págs. 397, 398, 399.

External features: Body cylindrical, slender; fastigium of vertex moderately long and acute, foveolae narrow; galeae of maxillae turned forward to meet or slightly overlap the margin of the labrum; tegmina and hind wings well developed, the latter rather brightly coloured (red); prosternal tubercle compressed; hind femur with dorsal and ventral basal lobes subequally produced; male terminalia specialized.

Principal phallic characters: Epiphallus specialized, bridge stout,

anterior projections closely set and greatly elongate, appendices large, widely divergent and arising from the lateral plates, latter broad, lophi short, strongly and acutely hooked, apices laterally directed; lateral lobes of ectophallus large and strongly sclerotized to form a 'hood'

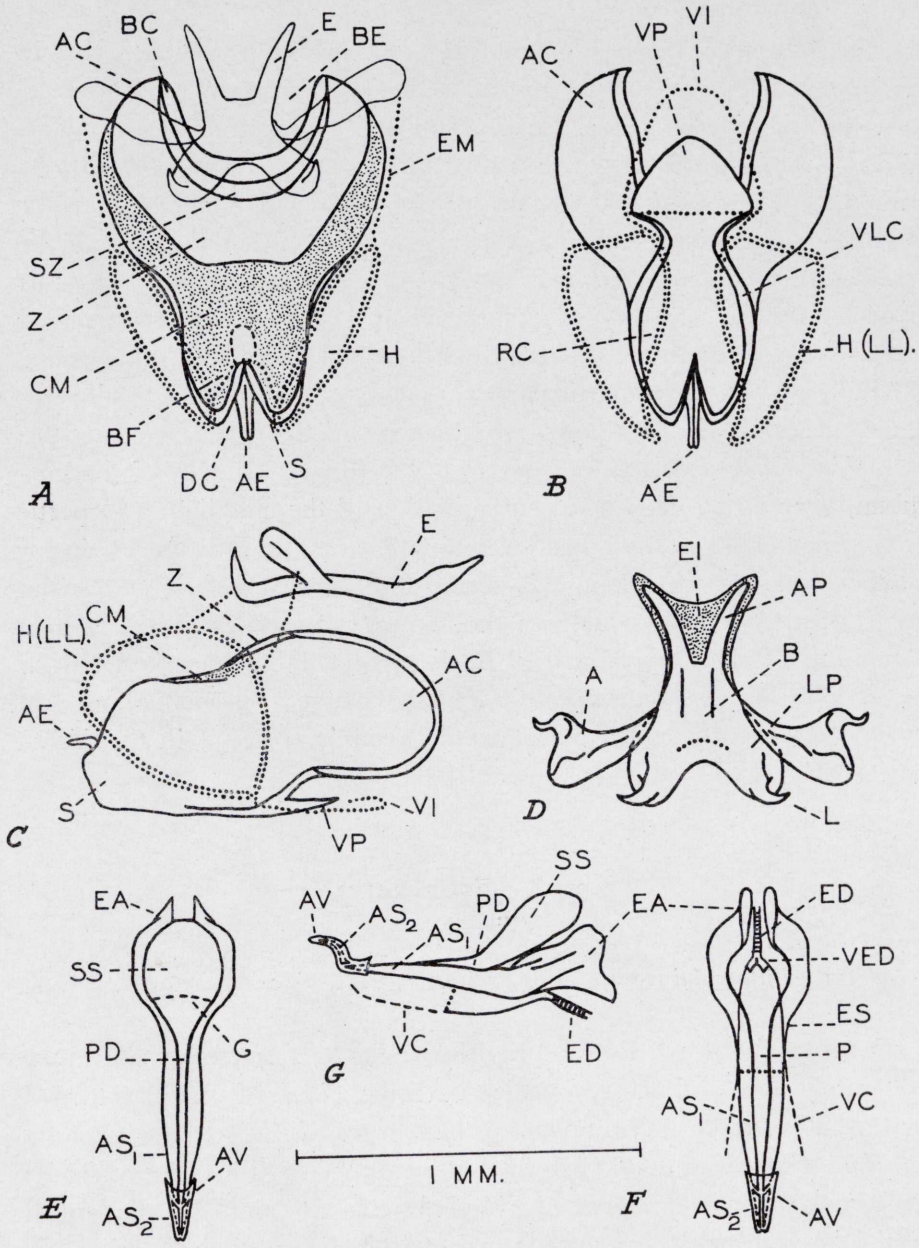

Fig. 1.—*Fijipyrgini: Fijipyrgus gracilis* Kevan, holotype, phallic structures. *A*, phallic complex, dorsal; *B*, the same, ventral; *C*, the same, from right; *D*, epiphallus, dorsal; *E*, endophallus dorsal; *F*, the same, ventral; *G*, the same, from right. For notation, see pp. 218-220.

laterally enveloping the apical part of the cingulum, central membrane extensive, zygoma of cingulum large and broad, suprazygomal plate small, basal emargination wide and deep, apodemal plates more or less rounded in lateral view, and without ventral processes, valves of cingulum virtually absent, ventral process of cingulum short; aedeagal sclerites rather slender, divided, apical parts bent upwards and rearwards, endophallic apodemes lacking definite dorsal inflections but with anteriorly directed ventral processes, spermatophore sac small, gonopore beyond the middle.

Concealed female structures: Unknown.

Distribution: Fiji Islands.

Included genus: Fijipyrgus Kevan, 1966 (only male examined [6]; adult female unknown).

Species examined: Fijipyrgus gracilis Kevan, 1966 (Viti Levu — Fig. 1) [Type species; = *F. secundus* Willemse, 1967 — see Kevan (1968 b)].

Other species: None known.

Some preliminary figures of the phallic structures of *F. gracilis* have already been published by Kevan (1966 b), who has referred to certain features, both external and phallic, that suggest possible relationships with various other tribes, notably *Verduliini* and *Mitricephalini* (and possibly *Tagastini*, Group B). The rather large central membrane of the ectophallus may also suggest some affinity with *Nereniini* through *Megra*. Although the *Fijipyrgini* are isolated geographically and exhibit certain specialized features, their apparent relationships with several other tribes suggests that they should be placed at the beginning of this series.

Tribe 2. Verduliini.

(Figs. 2 — 6).

[Geslacht *Acridium*] Groep IV. *Pyrgomorpha* Haan, 1847, *In* Temminck, *Verh. natuurl. Gesch. Ned. overz, Bezitt.*, XVIII (Zool., 7); 145 [no "Groep IV"], 148 (both *partim*).

[Limited] Family *Tryxalidae* Walker, 1870, *Cat. Derm. Salt. Brit. Mus.*, III, 499 *(partim)*; 1871, *Ibid.*, V (Suppl. 3): 101 *(partim)*.

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[6] "Examined" refers throughout to the *concealed* genitalic structures only. Every described species of *Pyrgomorphidae* except *Buyssoniella madecassa* Bolívar (unique ♀ lost) has been seen, at least by the most senior author.

Subfam. *Ort[h]acr[id]inae* Bolívar, 1905, *Bol. Soc. esp. Hist. nat.*, V, 278 *(partim)*.

Sect. *Orthacres* Bolívar, 1909, *Gen. Ins.*, XC, 4, 44 *(partim)*; Willemse, 1930, *Tijdschr. Ent.*, LXXIII, 74 *(partim)*.

Tribe *Verduliini* Kevan and Akbar, 1964, *Canad. Ent.*, XCVI, 1507, 1516, 1525; Kevan, 1966; *Pacif. Ins.*, VIII, 1, 2, 12, 397, 698; 1967, *Ibid.*, IX, 479.

Verduliononi [*sic*], Kevan, 1967, *Pacif. Entomologists' Newsletter*, I: (2), 6.

For group names applicable only to subtribe *Meubiliina*, see below.

External features: Body cylindrical; fastigium of vertex of moderate length to very short and obtuse; tegmina and hind wings fully developed to micropterous, latter not brightly coloured; prosternal tubercle conical or laterally tuberculate apically; metasternal pits comparatively small, sometimes with an indication of a rather straight suture joining them anteriorly (as in Group B); hind femora with dorsal and ventral basal lobes subequally produced, or the dorsal lobe more prominent; male terminalia unspecialized.

Principal phallic characters: Epiphallus of rather variable form but with prominent anterior projections, lophi widely spaced with dorsally directed hooks, or closely associated, united at the base, hooks long and directed more or less laterally; central membrane of ectophallus rather small, zygoma of cingulum small to very small, suprazygomal plate absent, basal emargination of cingulum extremely large and deep, apodemal plates tapered anteriorly in lateral view, pointed or with small ventral processes, rami of cingulum with internal inflected processes, sheaths, dorsal and ventral clefts, pseudoarch and ventral process of cingulum reduced or absent, valves of cingulum large, minutely denticulate and lateral or lateroventral in position; endophallus large, apices of aedeagal sclerites bent or furcate in lateral view, endophallic apodemes large with dorsal inflections well developed and ventral process, if any, small and posteriorly directed, aedeagal valves large to very large, sleeve-like, denticulate, spermatophore sac relatively very small with gonopore placed before the middle.

Concealed female structures: Postvaginal sclerite with characteristic heavily sclerotized ornamentation; columellae absent; receptaculum seminis with terminal part of spermathecal duct considerably or greatly dilated, spermathecal valve large, spermathecal appendage absent, caecum of spermatheca variable in size, simple, sometimes much reduced to a small but distinct, finger-like appendix.

Distribution: New Guinea, Moluccas, Philippines.

For recent accounts of the known members of this tribe, see Kevan (1963 c, 1966 b, 1967). Two subtribes may be recognized.

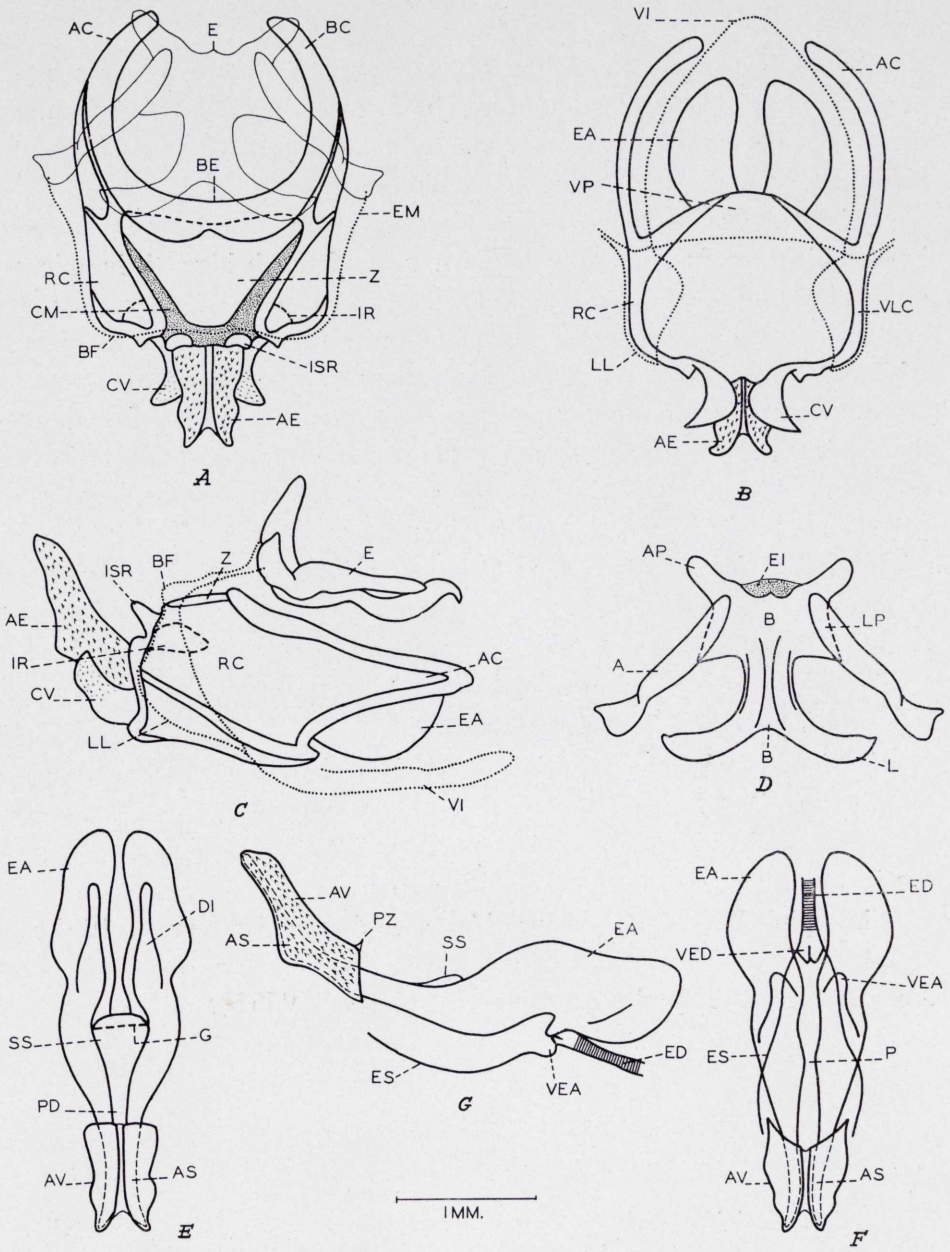


Fig. 2.—*Verduliini (Verduliina): Verdulia subcycloidea* Willemse, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

Subtribe *a.* VERDULIINA.
(Figs. 2, 4).

For synonymy, see above under *Verduliini.*

External features: Fastigium of vertex moderately produced; tegmina and hind wings macropterous, the former reaching or surpassing the hind knees; prosternal tubercle with lateral, subterminal bosses; hind femora with basal lobes subequally produced.

Principal phallic characters: Epiphallus with long, closely placed lophi which are fused basally to form part of the bridge, their apices directed more or less laterally, lateral plates with pointed externolateral expansions; apodemal plates of cingulum triangular in lateral view, without ventral processes, valves of cingulum comparatively smaller and more distinctly ventrolateral; aedeagal sclerites bent but not furcate at their apices, endophallic apodemes with dorsal inflections not posteriorly produced, but with small, backwardly directed ventral processes, aedeagal valves relatively not so large as in next subtribe.

Concealed female structures: Ornamentation of postvaginal sclerite in the forms of numerous, irregular, oblique ridges; caecum of spermatheca larger and wider than spermathecal vesicle, but rather short.

Distribution: New Guinea, Moluccas.

Included genus: Verdulia Bolívar, 1905.

Species examined: Verdulia subcycloidea Willemse, 1932 (Moluccas — Figs. 2, 4).

Other species: *Verdulia cycloidea* (Haan, 1842) (New Guinea) [Type species].

The epiphallus of *V. subcycloidea* was figured by Kevan (1963 c) and preliminary illustrations of the phallic and concealed female structures of the same species are given by Kevan (1966 b).

Subtribe *b.* MEUBELIINA nov.
(Figs. 3, 5 6).

[Fam. *Acrididae*] Subfam. *Catantopinae,* Sjöstedt, 1932, *Ark. Zool.,* XXIV, Ser. A (1): 32 *(partim);* Willemse, 1933, *Natuurhist. Maandbl.,* XXII, 73 *(partim);* 1956, *Publ. natuurhist. Genoots. Limburg,* VIII (1955), 3 *(partim).*

[Fam. *Acrididae,* Subfam. *Catantopinae*] *Tarbalei* Ramme, 1941, *Mitt. zool. Mus. Berlin,* XXV, 80 *(partim).*

Fam. *Catantopidae* F. Willemse, 1966, *Publ. natuurhist. Genoots. Limburg,* XVI, 36, 62 *(partim).*

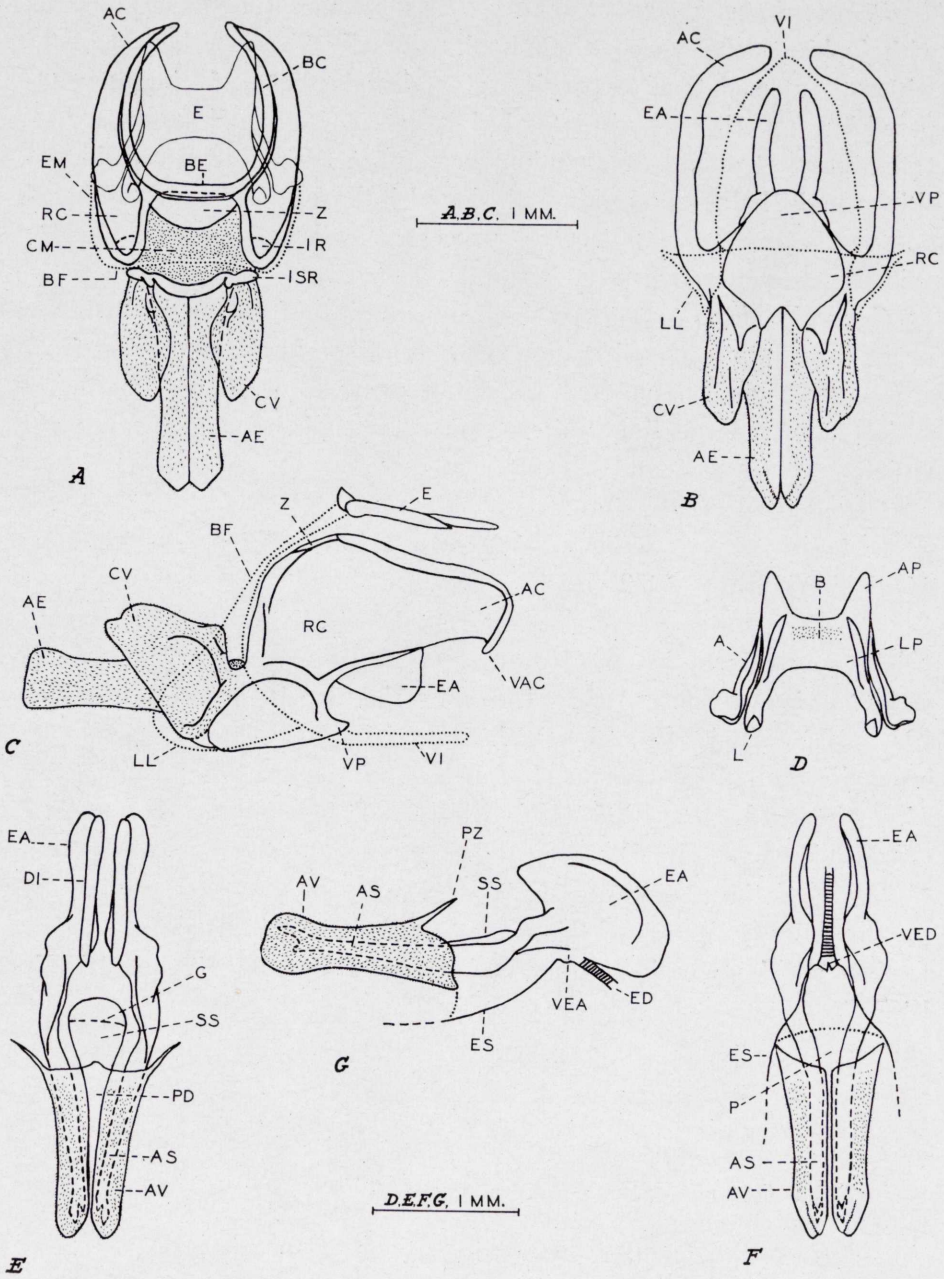


Fig. 3.—*Verduliini (Meubeliina): Meubelia atriantennis* (Willemse), holotype, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

External features: Fastigium of vertex very short and blunt; tegmina and wings reduced (former not reaching hind knees) to micropterous; hind femur with dorsal basal lobe projecting beyond the ventral one.

Principal phallic characters (in genus for which known): Epiphallus with lophi widely spaced, their hooks dorsally directed, lateral plates without externolateral expansions; apodemal plates of cingulum tapered but not triangular in lateral view, possessing small, anterior ventral processes, valves of cingulum very large and more lateral in position; endophallic apodemes with dorsal inflections strongly produced posteriorly but without ventral processes, aedeagal sclerites furcate apically, aedeagal valves very large.

Concealed female structures: Ornamentation of postvaginal sclerite in the form of strong reticulation; caecum of spermatheca varying from a well developed convoluted sac about as wide as the spermathecal vesicle to a reduced finger-like terminal appendix of the spermathecal vesicle.

Distribution: Philippines.

Included genera: Spinacris Willemse, 1933 (only female known); *Meubelia* Willemse, 1932.

Species examined: Spinacris viridis Willemse, 1933 (Mindanao) [Type species]; *S. elegans* Kevan, 1966 (Luzon — Fig. 5); *Meubelia atriantennis* (Willemse, 1932) (Luzon — Fig. 3); *M. gracilis* Willemse, 1932 (NE. Mindanao and neighbouring islands) [Type species]; *M. bruneri* Kevan, 1967 (Samar, I.); *M. bakeri* Kevan, 1967 (Biliran I.); *M. schistacra* Kevan, 1967 (NW. Mindanao); *M. bivittata* Kevan, 1967 (N. Mindanao — Fig. 6).

Other species: None known.

Preliminary figures of the concealed genitalia of all species, so far as they are known, have already been published by Kevan (1966 b, 1967).

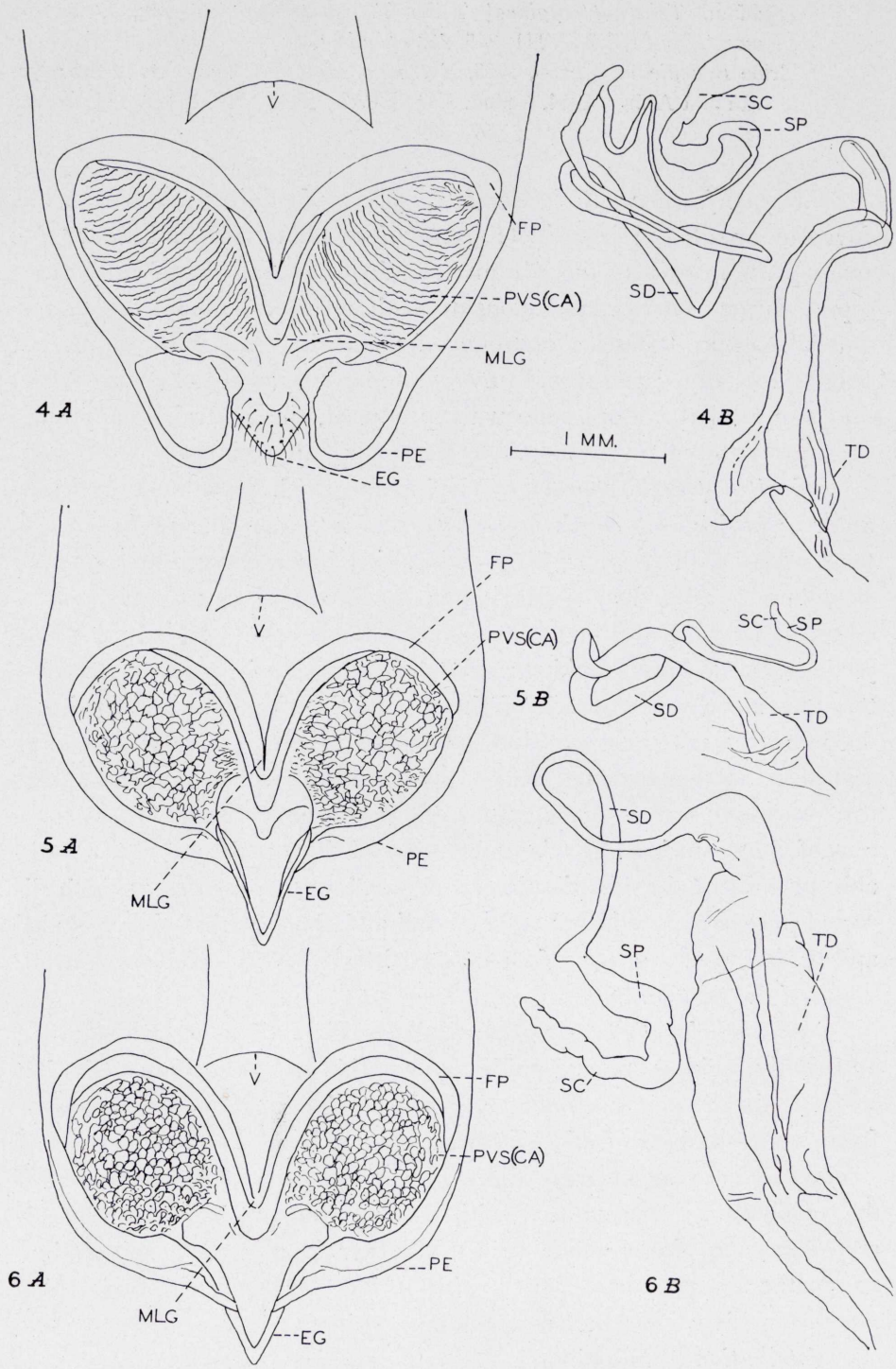
Tribe 3. Brunnieellini.

(Figs. 7, 8).

Tribu *Trigonopteriginos* Bolívar, 1905, *Bol. Soc. esp. Hist. nat.*, V, 298, 299 *(partim)*.

Sect. *Systellae* Bolívar, 1909, *Gen. Ins.*, XC, 4, 51, 52 *(partim)*.

Subfam. *Trigonopteryginae* Dirsh, 1952, *Ann. Mag. nat. Hist.* (12), V, 82, 83 *(partim)*.



Figs. 4-6.—*Verduliini*, female structures: 4) *Verdulia subcycloidea* Willemse; 5) *Spinacris elegans* Kevan, holotype; 6) *Meubelia bivittata* Kevan, paratype, *A*, subgenital plate, dorsal, *B*, receptaculum seminis. For notation, see pp. 218-220.

[Subfam. *Trigonopteryginae*] Tribe *Trigonopterygini* Kevan, 1952, *Ent. mon. Mag.*, LXXXVIII, 265, 267 *(partim)*.

Tribe *Brunniellini* Kevan, 1963, *Ent. mon. Mag.*, XCVIII (1962), 213; Kevan and Akbar, 1964, *Canad. Ent.*, XCVI, 1507, 1512, 1514, 1524; Kevan 1966, *Pacif. Ins.*, VIII, 397, 399.

External features: Body elongate, slender; fastigium of vertex acute, foveolae broad and indistinct; galae of maxillae turned forwards to overlap the margin of the labrum; tegmina and hind wings fully developed, former narrow and elongate with an apical mucro and a few small knot-like tubercles on some of the main veins, hind wings not brightly coloured; prosternal tubercle bilobed; hind femora with dorsal and ventral basal lobes subequally produced, the ventral, if anything, the more prominent; abdominal terminalia unspecialized.

Principal phallic characters: Epiphallus with prominent, rod-like, anterior projections, weak appendices and a rather shallow bridge, lateral plates with peculiar, large, wing-like, inner expansions, lophi of an unique rod-like form with irregularly toothed lateral margins, attached to the lateral plates and appreciable distance behind the anterior projections, apical hooks lacking; central membrane of ectophallus restricted, zygoma covering much of the rest of the cingulum and having a deep median posterior excision, basal emargination of cingulum large and deep, apodemal plates bluntly pointed in lateral view, without ventral processes, valves of cingulum and suprarami absent, ventral process of cingulum broadly triangular; endophallic apodemes with reasonably prominent dorsal inflections and small ventral processes, both directed posteriorly, aedeagal valves small and short, with rather rounded apices, spermatopore sac of moderate size, pyriform, gonopore in advance of the middle.

Concealed female structures: Subgenital plate long and narrow, apparently lacking an egg-guide (unless this has been damaged), but with a pair of curious elongate rod-like thickenings running forwards from where its base would be (these seem to combine the functions of columellae and contact areas and apparently match the peculiar lophi of the epiphallus); spermatheca with a small, subterminal, laterally directed caecum, from which arises a rather long, coiled, subterminal spermathecal appendage, latter with a few short, basal, finger-like, secondary diverticula and a small but distinct apical bulb.

Distribution: Philippines.

Included genus: Brunniella Bolívar, 1905.

Species examined: Brunniella antistes Bolívar, 1905 (Sibayan and Mindanao — Figs. 7, 8) [Type species].

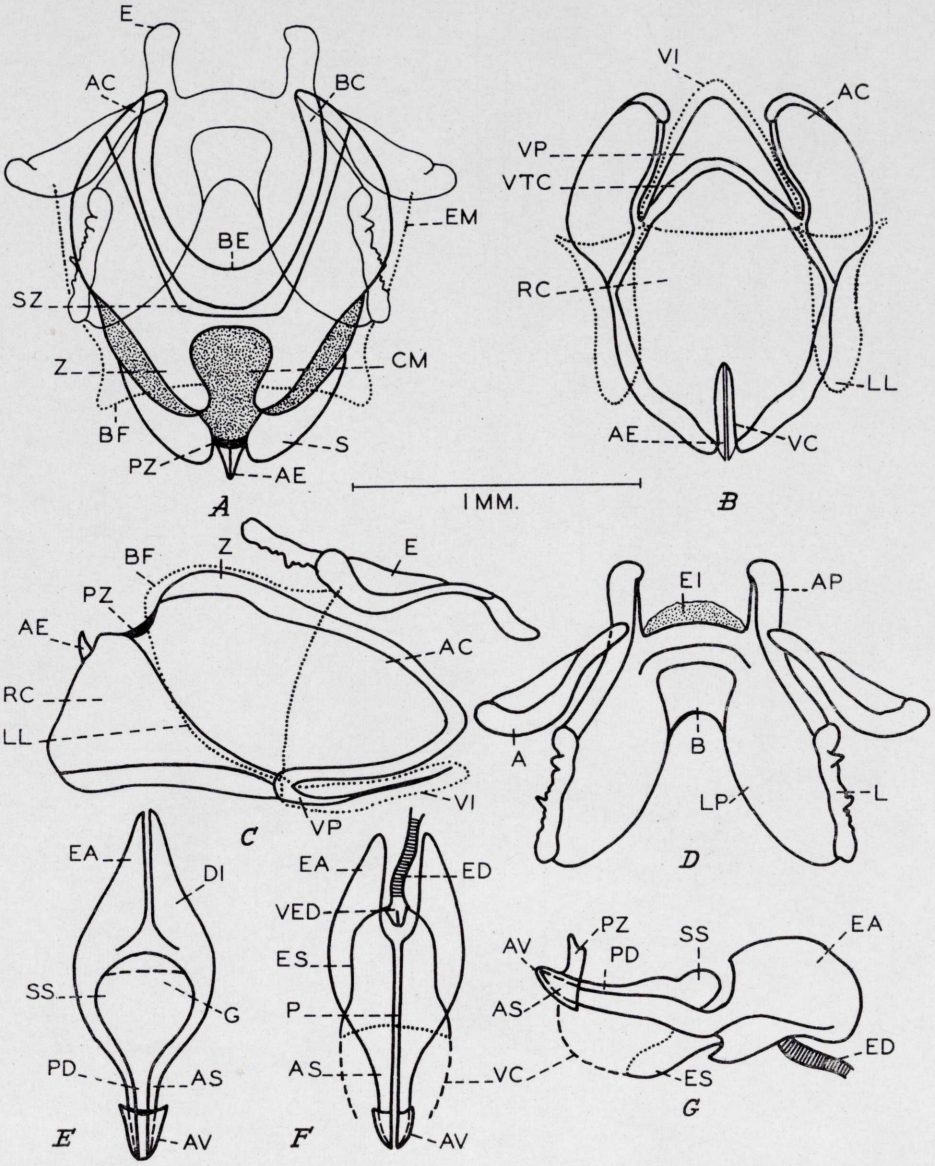
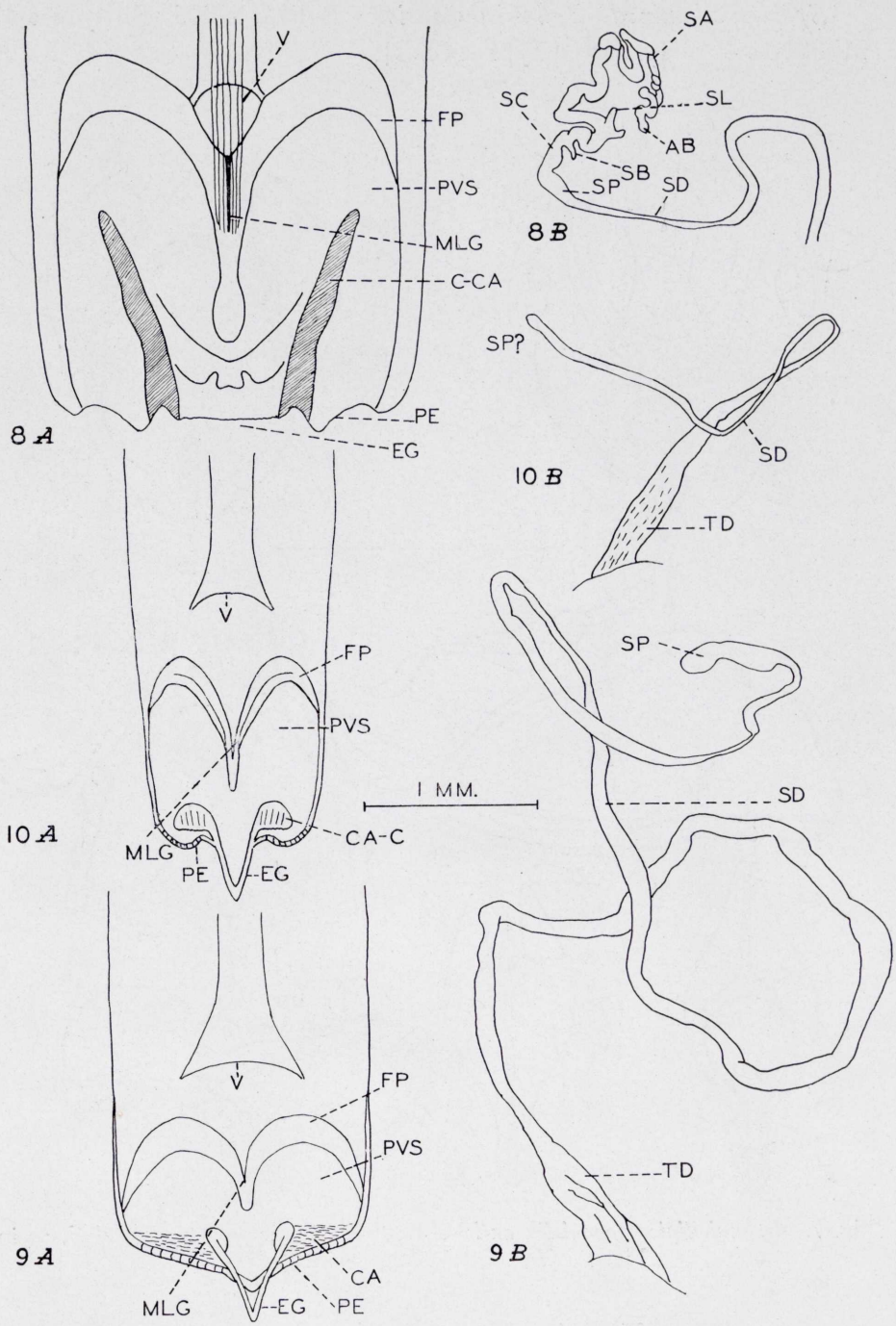


Fig. 7.—*Brunniellini: Brunniella antistes* Bolívar, phallic structures. *A-G*, as in Fig. 1. For notation, see pp. 218-220.

Other species: None known.

The recent literature on the tribe is that of Kevan (1957), who recognized *B. antistes* as belonging to the *Pyrgomorphidae* (in the mo-



Figs. 8-10.—*Brunniellini* and *Psednurini*, female structures. 8) *Brunniella antistes* Bolívar, holotype (it is not certain if the egg-guide is absent or damaged); 9) *Propsednura nana* Rehn; 10) *Psednura musgravei musgravei* Rehn. *A-B* as in Figs. 4-6. For notation, see pp. 218-220.

dern sense), and Kevan (1963 a), who discovered the male and figured its epiphallus. Certain features of this anomalous tribe suggest some affinity with the *Verduliina* — notably the bilobed prosternal tubercle, the pointed apodemal plates, the large, deep basal emargination of the cingulum and the backwardly directed ventral processes of the endophallic apodemes. The very slender build and forwardly turned galeae are suggestive of the *Psednurini* (Kevan, 1957) although these may be merely convergent characters. That tribe, however, has little in common with any other, but it is also characterized by a rather large, deep basal emargination of the cingulum, somewhat pointed apodemal plates and the absence of valves of the cingulum, so there may be some relationship.

Tribe 4. Psednurini.

(Figs. 9-12).

[Fam. *Eumastacidae*] Subfam. *Psednurinae* Burr, 1903, *Gen. Ins.*, XV, 3, 22 *(partim)*; C. Bolívar y Pieltain, 1930, *Trab. Mus. Cienc. nat. Madrid* (Zool.), XLVI, ix *(partim)*.

[Fam. *Acridiidae*] Subfam. *Truxalinae* Kirby, 1910, *Syn. Cat. Orth.*, III, 90 *(partim)*.

Fam. *Truxalidae* Sjöstedt, 1920, *Ark. Zool.*, XII (20), 5 *(partim)*.

Fam. *Acridiidae* Sjöstedt, 1921, *K. svensk. Vetensk. Akad. Handl.* (2), LXII (3), 83, 300 *(partim)*; 1931, *Ark. Zool.*, XXIII, Ser. A (11), 3, 14 *(partim)*; 1935, *K. svensk. Vetensk. Akad. Handl.* (3), XV (2), 59, 175 *(partim)*.

[Fam. *Acrididae*] Subfam. *Psednurinae* Brues and Melander, 1932, *Bull. Mus. comp. Anat.*, LXXIII, 56; Brues, Melander and Carpenter, 1954, *Ibid.*, CVIII, 101 [as the only genus mentioned in *Psednura*, these citations are not *partim*].

[Fam. *Acrididae*] Subfam. *Catantopinae* Key, 1937, *Ann. S. Afr. Mus.*, III, 137 *(partim)*; Slifer and Uvarov, 1938, *Proc. R. ent. Soc. London* (A), 13, 114 *(partim)*.

Tribe *Psednurini* Rehn, 1953, *Grassh. Locusts Austr.*, II, 18, 20, 23, 24, 25, 26, 222, 223; Kevan, 1954, *Ent. mon. Mag.*, XC, vii, viii; 1957; *Nova Guinea* (n. s.), VIII, 197, 202; 1959, *Publ. cult. Cia. Diam. Ang.*, XLIII, 203; Rehn and Grant, 1959, *Ent. News*, LXX, 248; Kevan, 1961, *Ent. mon. Mag.*, XCVI, 204; 1963, *Ibid.*, XCVIII (1962), 211, 213; Kevan and Akbar, 1964, *Canad. Ent.*, XCVI, 1507, 1514, 1524; Kevan, 1966, *Pacif. Ins.*, VIII, 398; Blackith and Blackith, 1966, *Austr. J. Zool.*, XIV, 1040; Key, 1969, *Ibid.*, XVII, 411.

[Fam. *Eumastacidae*] Unterfam. *Miraculinae* Beier, 1956, *Bronn's Kl. Ord. Tierr.*, V (3), 6, Buch: 262 *(partim)*.

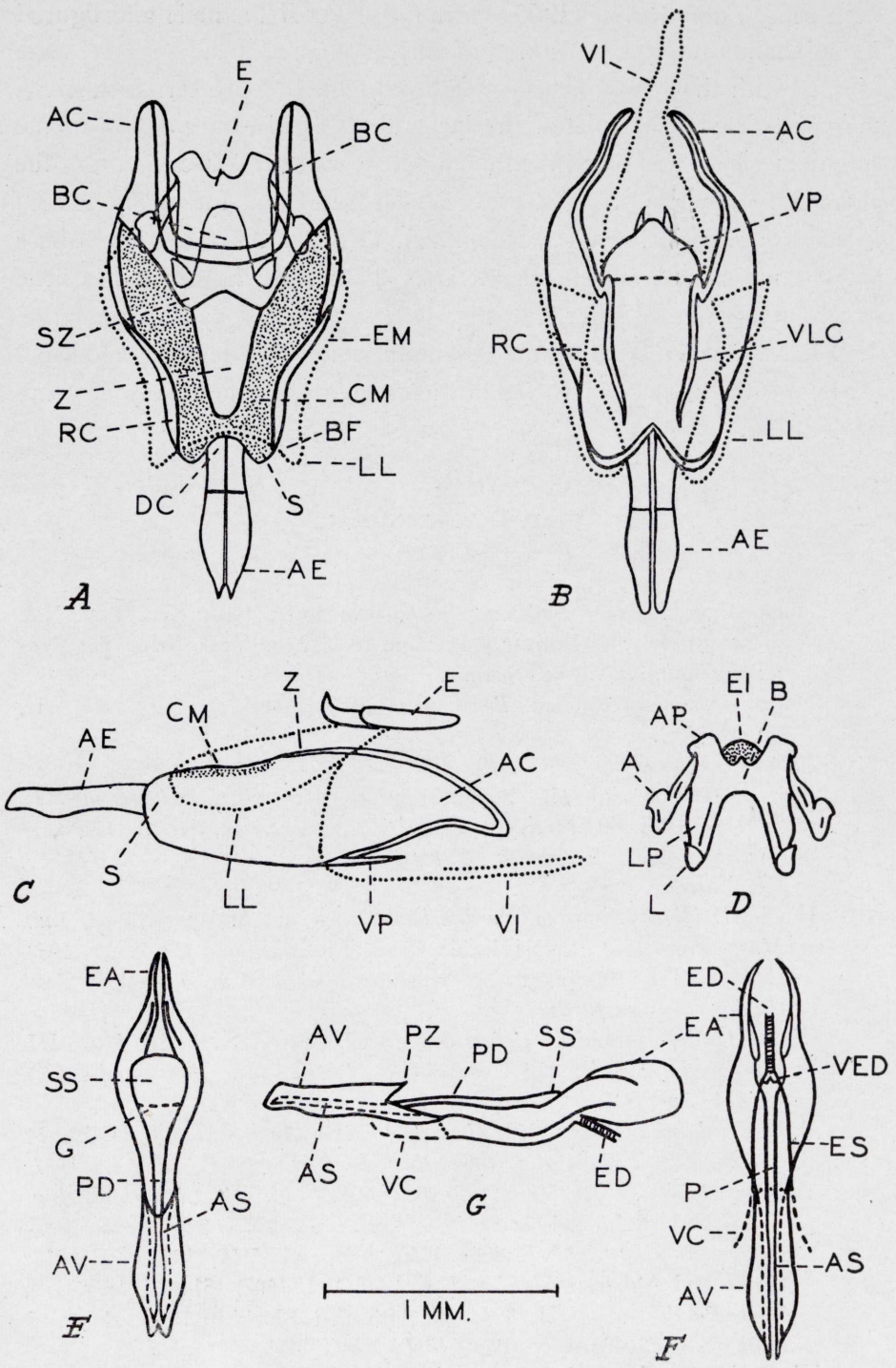


Fig. 11.—*Psednurini: Propsednura nana* Rehn, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

External features: Body very long and slender, bacilliform; fastigium of vertex greatly elongate, foveolae poorly defined; galeae of maxillae strongly modified, turned forward over the labrum; tegmina and hind wings scale-like or wanting [7]; prosternal tubercle very reduced; hind femur very slender with lower internal carina raised nearly up to the middle of the internal face so that, at rest, the hind tibiae can virtually be tucked out of sight; subgenital plate of male greatly elongated, forming a dagger-like projection; epiproct of immature stages similarly produced.

Principal phallic characters: Epiphallus rather unremarkable but with prominent anterior projections and a shallow bridge, hooks of lophi dorsally to dorsolaterally directed, appendices sometimes trilobate at their apices; central membrane of ectophallus rather extensive, zygoma of cingulum fairly small, variable in shape, broad to narrowly triangular, suprazygomal plate present, basal emargination of cingulum wide and deep, apodemal plates in lateral view rather narrow, bluntly pointed, without ventral processes; valves of cingulum absent, ventral process of cingulum short or wanting; ventral cleft, and dorsal cleft if present, notch-like; aedeagal sclerites slender, moderately to very elongate; endophallic apodemes rather small, simple or with small backwardly directed dorsal processes, aedeagal valves fairly to very long and somewhat sleeve-like, considerably produced forward ventrally, apices rather obliquely truncated with low subterminal ventral protuberances; spermatophore sac rather small, pyriform, gonopore in a median position.

Concealed female structures: Subgenital plate greatly elongate, egg-guide sometimes rather small, posterior edge crenulated; columellae present; receptaculum seminis reduced, spermatheca consisting only of a small spermathecal vesicle or of a tiny bulb resembling the apical bulb of the spermathecal appendage in certain other groups (possibly homologous with this), spermathecal duct long and coiled, or short, terminal part dilated.

Distribution: Australia.

Included genera: Propsednura Rehn, 1953; *Psednura* Burr, 1907.

Species examined: Propsednura nana Rehn, 1953 (S. W. Western Australia to W. Victorial and S. W. New South Wales — Figs. 9, 11);

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[7] Rarely, in *Propsednura nana,* tegmina and hind wings may be almost fully developed, the latter violet.

Psednura musgravei musgravei Rehn, 1953 (New South Wales — Figs. 10, 12).

Other species and subspecies: Propsednura eyrei Rehn, 1953 (S. Western Australia to Kangaroo I) [Type species; = *P. hesperus* Rehn,

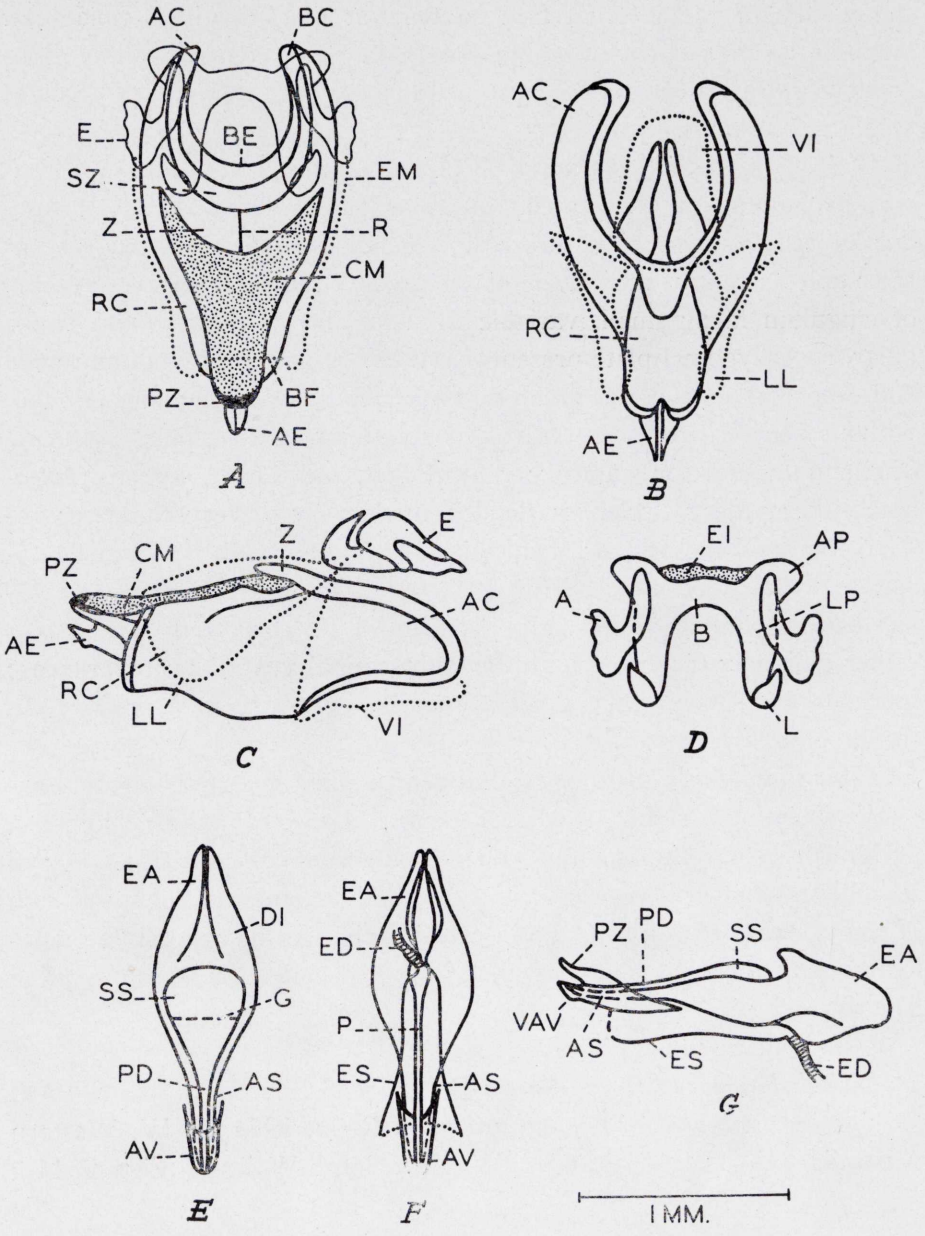


Fig. 12.—*Psednurini: Psednura musgravei musgravei* Rehn, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

1953]; *Psednura pedestris collina* Rehn, 1953 (interior of Tasmania), *P. p. pedestris* (Erichson, 1842) (coastal Tasmania, Victoria, South Australia) [Type species; = *P. lanceolata* Rehn, 1953], *P. musgravei angustissima* Rehn, 1953 (E. Queensland, NE. New South Wales).

Recent taxonomic work on this tribe is that of Rehn (1953), but it has been considerably amended by Key (1969). The tentative recognition of subspecies is somewhat of a compromise after discussions with Dr. Key and pending his further studies. Dirsh (1956) has illustrated the epiphallus of what he calls *Betisca pedestris*. No other figure of the concealed genitalia has been published. This tribe has certain similarities to the *Brunniellini* (see above), but the deep basal emargination of the cingulum, and the sleeve-like aedeagal valves of *Propsednura*, suggest some affinity with the *Verduliini* also.

Tribe 5. Mitricephalini.

(Figs. 13-16).

Subfam. *Or[h]acr[id]inae* Bolívar, 1905, *Bol. Soc. esp. Hist. nat.*, V, 278 *(partim)*.

Sect. *Orthacres* Bolívar, 1909, *Gen. Ins.*, XC, 4, 44 *(partim)*; Willemse, 1930, *Tijdschr. Ent.*, LXXIII, 74 *(partim)*.

[Fam. *Acridiidae*] Subfam. *Cyrtacanthacr[id]inae* Kirby, 1910, *Syn. Cat. Orth.*, III, 358 *(partim)*.

[Fam. *Acridiodea*] Subfam. *Cyrtacanthacr[id]inae*, Group *Cranaeae* Willemse, 1921, *Zool. Meded.*, VI, 6, 21 *(partim)*.

[Fam. *Acrididae*] Subfam. *Catantopinae* Willemse, 1930, *Tijdschr. Ent.*, LXXII, 103, 209 *(partim)*; Miller, 1934, *J. Fed. Mal. St. Mus.*, XVII, 531 *(partim)*; Chopard, 1938, *Encycl. Ent.* (A), XX, 22 *(partim)*.

Tribe *Mitricephalini* Kevan and Akbar, 1964, *Canad. Ent.*, XCVI, 1507, 1514, 1524, 1528 *(partim)*; Kevan, 1965, *Proc. XII, Int. Ent. Congr.*, London, 1964, 442 *(partim)*; 1966, *Pacif. Ins.*, VIII, 397 *(partim)*.

The last three citations are listed as referring only in part to this tribe because *Kuantania* Miller, 1935, has now been removed from it to the *Orthacridini* (Series III).

External features: Body elongate-cylindrical; fastigium of vertex very short and blunt; median ocellus lacking; tegmina and hind wings fairly well developed, but leaving much of the abdomen exposed and not extending to more than about two-thirds of the length of the hind femur, hind wings usually coloured (red or yellow), often with a dark-

border; prosternal tubercle transversely compressed; hind femora with dorsal and ventral basal lobes subequally produced; posterior metatarsi rather elongate; male abdominal terminalia specialized.

Principal phallic characters: Specialized and rather variable; epi-

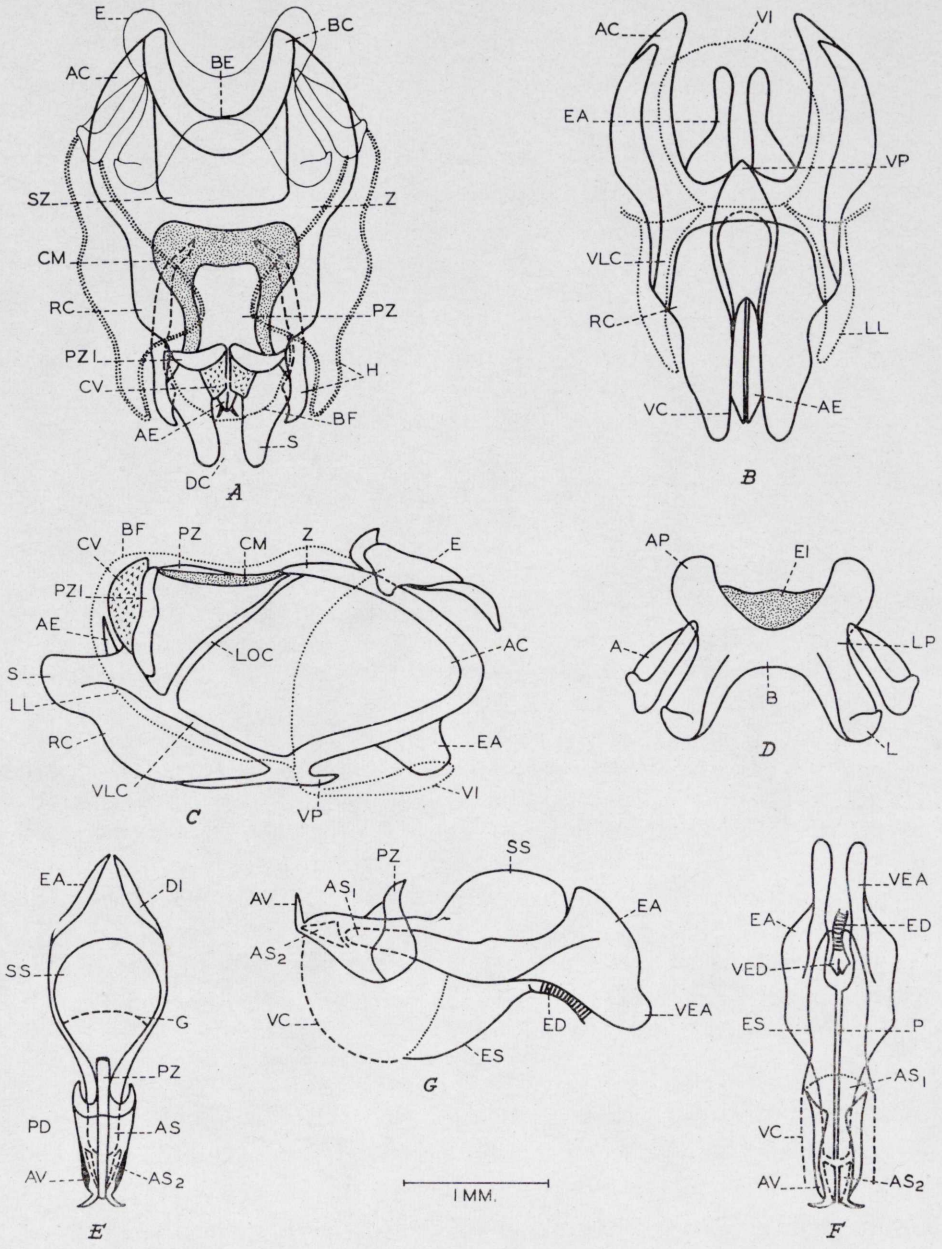


Fig. 13.—*Mitricephalini: Mitricephaloides rhodoptera* (Miller), phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

phallus with diverging lateral plates, generally of two forms, either with prominent anterior projections or with these virtually absent, for-

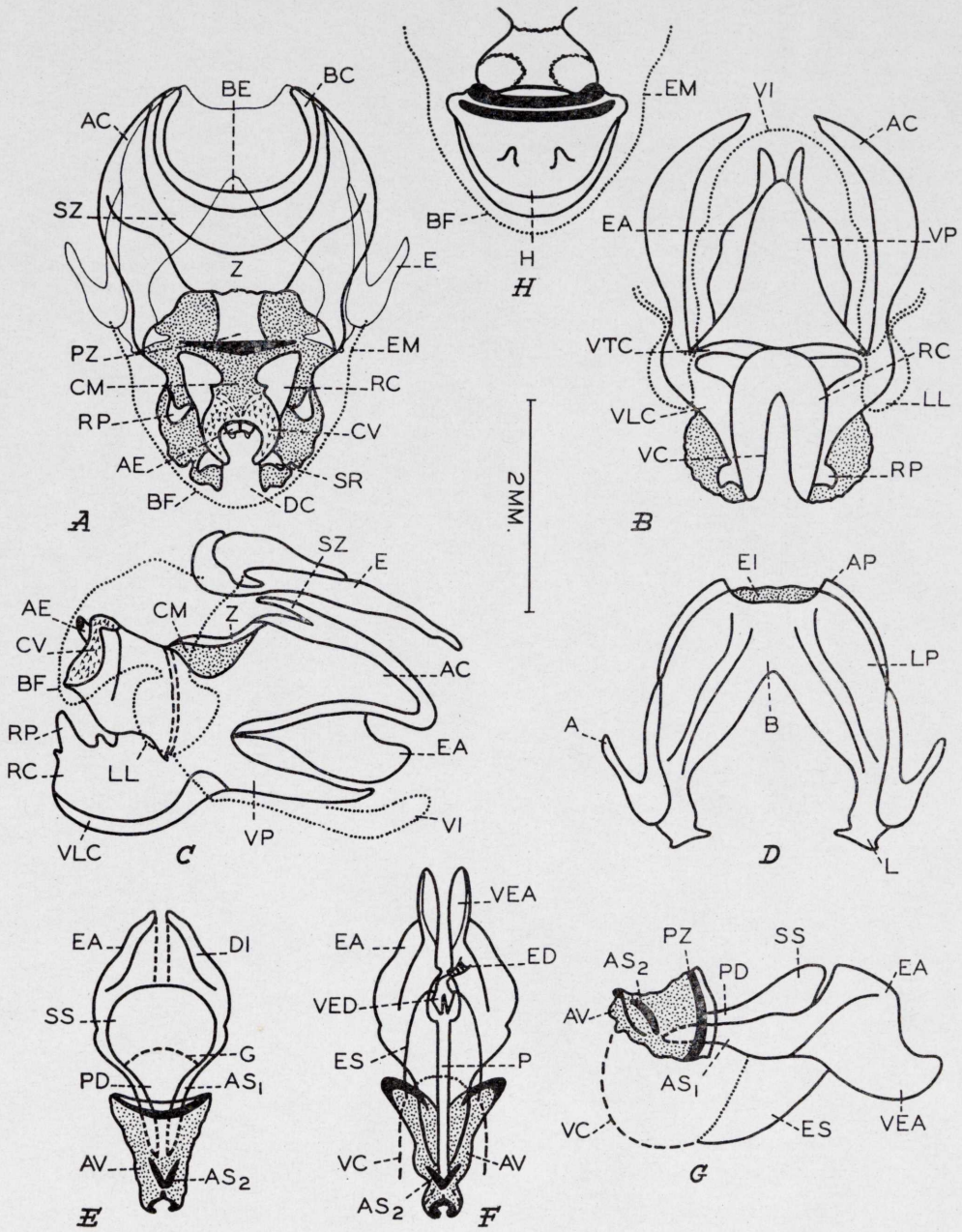


Fig. 14.—*Mitricephalini: Mitricephala javanica* Kevan, holotype, phallic structures. *A-G* as in Fig. 1 (*A* with apical part of dorsal ectophallic membrane and associated structures removed), *H,* apical part of ectophallic membrane and associated structures. For notation, see pp. 218-220.

mer with unremarkable, dorso-laterally directed lophi, latter with atypical incurved, truncated corresponding structures, bridge in both forms rather shallow; ectophallic membrane with a complicated sclerotized 'hood', either lateral, incorporating the lateral lobes, or dorsally covering the apex of the cingulum, central membrane rather restricted, zygoma of cingulum broad but short, suprazygomal plate usually rather small, basal emargination of cingulum moderately deep, apodemal plates in lateral view more or less rounded or triangular anteriorly, without ventral processes, valves of cingulum prominent and denticulate, rami and associated structures variously specialized, pseudoarch large, ventral process of cingulum large and triangular to virtually absent; endophallus rather short, aedeagal sclerites divided apically, endophallic apodemes with dorsal inflections fairly well developed, rather broad in lateral view, angular dorsally and with broad ventral processes directed anteriorly, aedeagal valves rather large and deep with specialized ('hooked') apices, spermatophore sac moderately large, subspherical, gonopore somewhat behind he middle.

Concealed female structures: Subgenital plate with a short egg-guide, posterior part of the post-vaginal sclerite marked off as two broad, band-like contact areas; columellae absent or slightly indicated; spermatheca short, open S-shaped, spermathecal appendage absent, caecum of spermatheca short and terminal, not differentiated from spermathecal vesicle, spermathecal duct simple with a short terminal dilation.

Distribution: Indonesia, Malaysia.

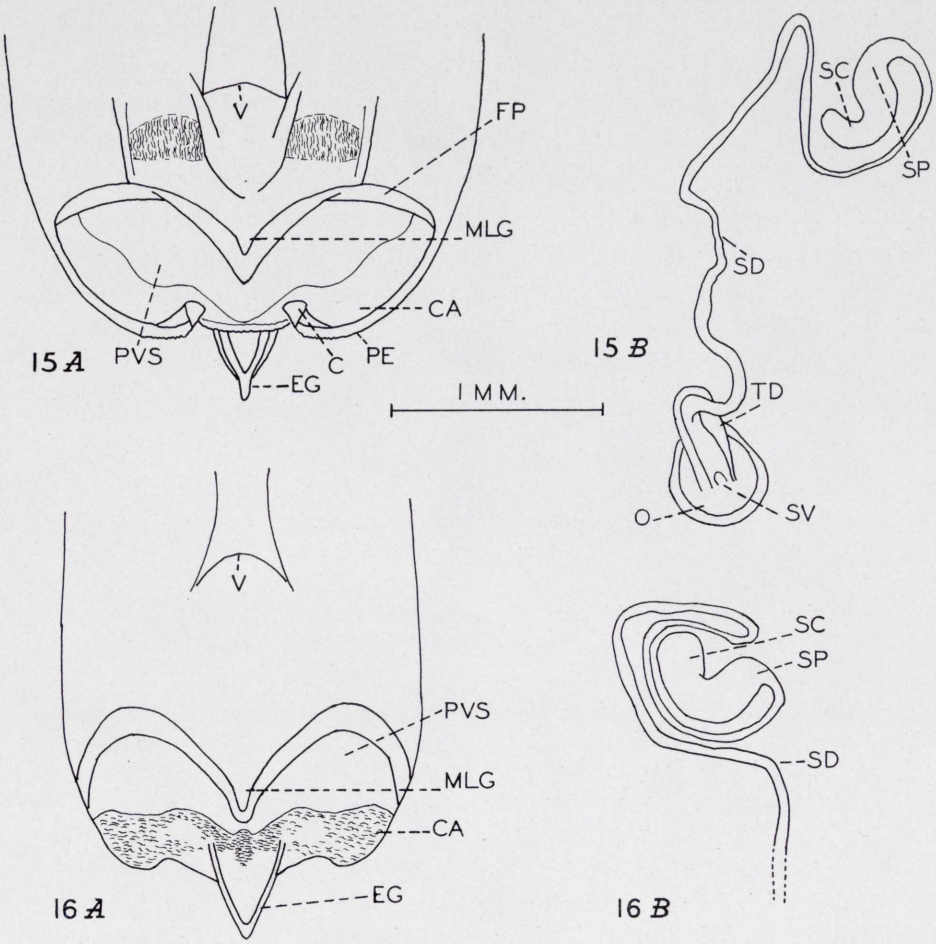
Included genera: Mitricephaloides Kevan, 1963; *Mitricephala* Bolívar, 1898 [*Kuantania* Miller, 1935, has been removed elsewhere, see above].

Species examined: Mitricephaloides rhodoptera (Miller, 1934) (Malay Peninsula — Figs. 13, 15) [Type species]; *Mitricephala dohrni* (Bolívar, 1905) (Sumatra — Fig. 16); *M. javanica* Kevan, 1963 (Java — Fig. 14).

Other species: Mitricephaloides rubrosignatus (Ramme, 1941) (Borneo); *Mitricephala vittata* Bolívar, 1898 (Mentawei Is.) [Type species], *M. milleri* Ramme, 1941 (Malay Peninsula).

The various species are discussed by Kevan (1963 c), who gives figures of the epiphallus of *Mitricephala javanica* and *Mitricephaloides rhodoptera*. This tribe stands somewhat in isolation from the preceding ones, although a comparison of characters will indicate one or two common features. As with other forms having specialized geni-

talia, it is difficult to detect relationships. The divided aedeagal sclerites and the 'hood' are notable features. Both occur in the *Fijipyrgini* and in the *Geloiini* of Madagascar to which the *Mitricephalini* bear other, possibly convergent, resemblances, such as the body form and



Figs. 15-16.—*Mitricephalini*, female structures. 15) *Mitricephaloides rhodoptera* (Miller); 16) *Mitricephala dohrni* Bolívar. *A-B* as in Figs. 4-6. For notation, see pp. 218-220.

lack of a median ocellus. It may be that there is a phylogenetic relationship between these two tribes and for this reason, the *Geloiini* will be treated next. It is also possible that there is some affinity between *Mitricephalini* and *Orthacridini*. The reduced spermatheca, however, is somewhat more reminiscent of *Verduliini*.

SERIES II.

Members of this series of tribes seem to be reasonably closely related to each other although this is not at all obvious from their phallic structures. All included species are from Madagascar and all are apterous or strongly micropterous. They have one seemingly trivial feature in common that is not found in other *Pyrgomorphidae*. The frontal costa immediately below the fastigium of the vertex is excised in profile before sloping backwards to the frons proper. An exception is *Gymnohippus* in which the relevant part of the frontal costa is vertical, not excised, but this condition is also unique for Group A and is only found in *Pyrgomorphidae* of Group B in some *Chrotogonini*, to which *Gymnohippus* otherwise bears no close resemblance. The condition in this genus is clearly derived from the excised conformation and is associated with the near-vertical general frontal profile.

TRIBE 6. GELOIINI.
(Figs. 17-20).

[Tribus *Pyrgomorphii* (= *Pyrgomorphidae)*] Stirps *Geloius* Saussure, 1899, *Abh. Senckenb. Naturf. Ges.*, XXI, 637 *(partim)* [♂ is *Sagittadidini*].

Subfam. *Geloiinae* Bolívar, 1905, *Bol. Soc. esp. Hist. nat.*, V, 284 *(partim)*.

Sect. *Geloii* Bolívar, 1909, *Gen. Ins.*, XC, 4, 50 *(partim)*; Johnston, 1956, *Annot. Cat. Afr. Grassh.*, 200 *(partim)*.

Geloius Group, Dirsh, 1963, *Bull. Brit. Mus. (nat. Hist.) Ent.*, XIV, 93 *(partim)* [*Geloii*, Strips *(sic) Geloius* and *Geloiinae* all mentioned p. 86 in discussion].

Tribe *Geloiini* Kevan, Singh and Akbar, 1964, *Proc. Acad. nat. Sci. Philad.*, CXVI, 232 *(partim)* [*Geloii* and *Geloiinae* also indicated as synomyms]; Descamps and Wintrebert 1966, *Eos, Madrid*, XLII, 108; Kevan, 1968, *Ibid.*, XLIII, 576, 579.

Tribe *Pseudogeloiini* Kevan and Akbar, 1964, *Canad. Ent*, XCVI, 1507, 1512, 1524; Kevan, 1965, *Proc. XII, Int. Congr. Ent.*, London, 1964, 442; 1966, *Pacif. Ins.*, VIII, 397 [synonymized, Descamps and Wintrebert, 1966, *Eos, Madrid*, XLII, 108].

External features: Body elongate, cylindrical, integument usually striated, mottled greyish-brown; fastigium of vertex moderately short, triangular to long and acute; female antennae flattened and usually

somewhat expanded; tegmina and hind wings absent or minute and scale-like; male terminalia, or at least the apices of the cerci, specialized.

Principal phallic characters: Epiphallus unspecialized, with reduced

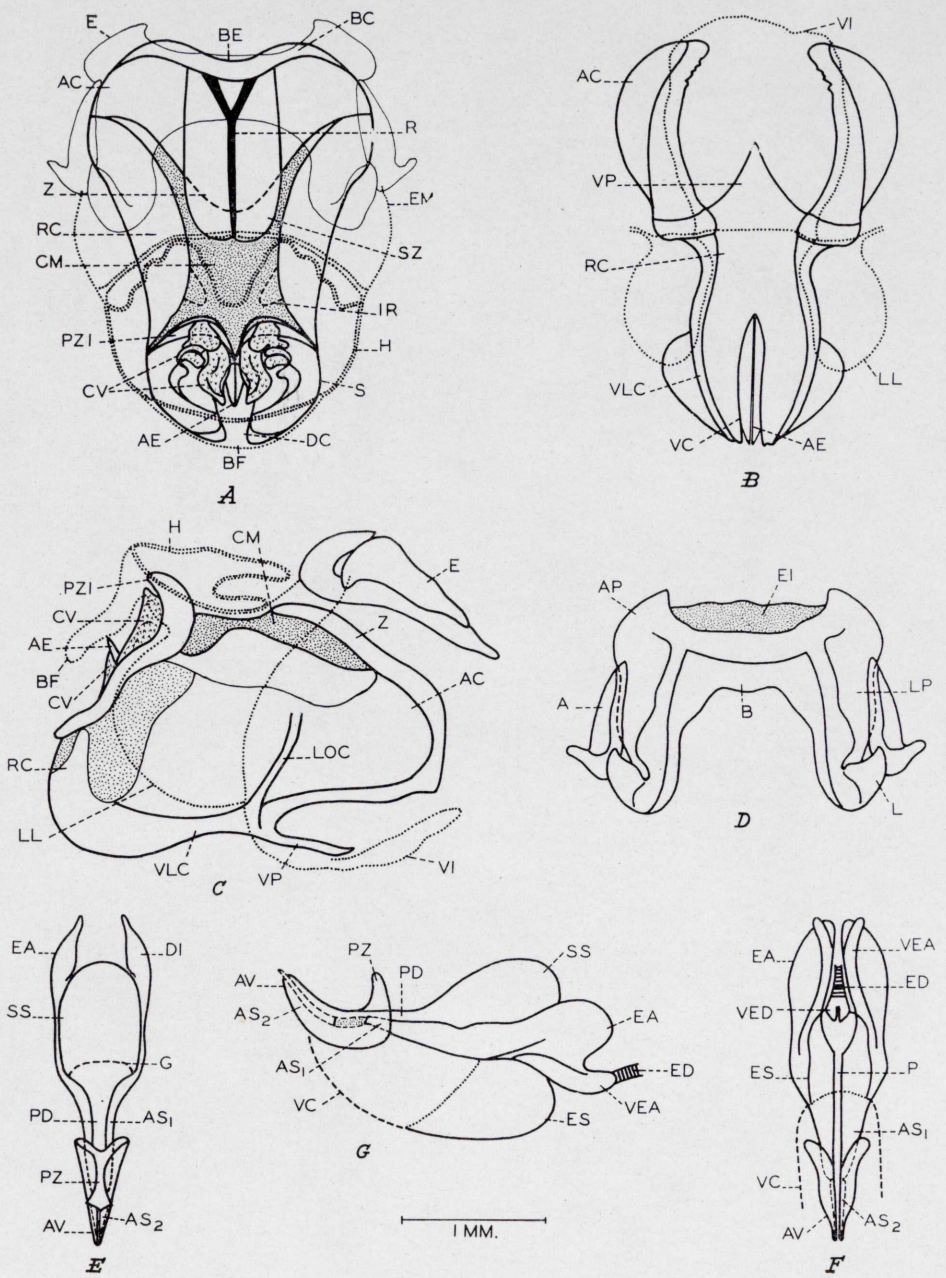


Fig. 17.—*Geloiini: Pseudogeloius rilictus* Dirsh, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

anterior processes, bridge moderately slender, appendices weak, lophi with dorsally or dorsolaterally directed apices; ectophallic membrane dorsally sclerotized, at least to some extent, to form a 'hood' over the

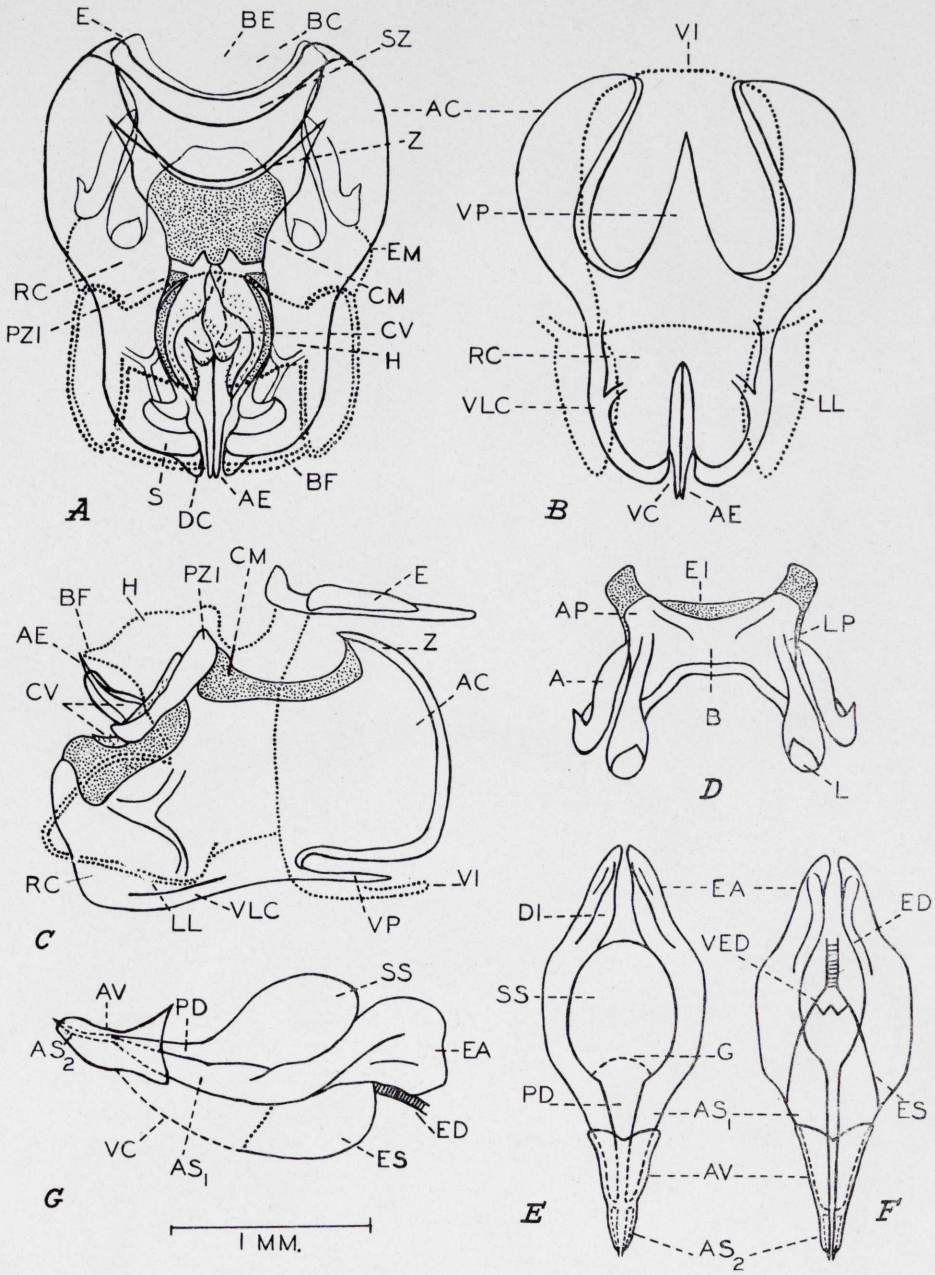


Fig. 18.—*Geloiini: Geloius nasutus* Saussure, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

apical part of the cingulum, central membrane rather elongate and narrow, somewhat constricted or subdivided, zygoma of cingulum short, suprazygomal plate long and narrow or short and moderately broad, basal emargination very shallow, apodemal plates somewhat quadrangular in lateral view, without obvious traces of ventral processes, valves of cingulum relatively large, complex in form and denticulate, ventral process of cingulum short or of moderate length, acutely pointed; aedeagal sclerites of moderate proportions, divided, apical parts attached to the main body of the sclerites by a membranous flexure, endophallic apodemes without strong dorsal inflections, with or without distinct anteriorly directed ventral processes, spermatophore sac rather large, oval, gonopore distinctly beyond the middle, aedeagal valves conical, pseudoarch poorly developed.

Concealed female structures: Posterior edge of subgenital plate slightly crenulated; egg-guide short or of medium length; columellae and contact areas absent; spermatheca forming a single, rather short, S-shaped sac, caecum not well distinguished from spermathecal vesicle, spermathecal duct narrow, of moderate length with small, short, terminal dilation.

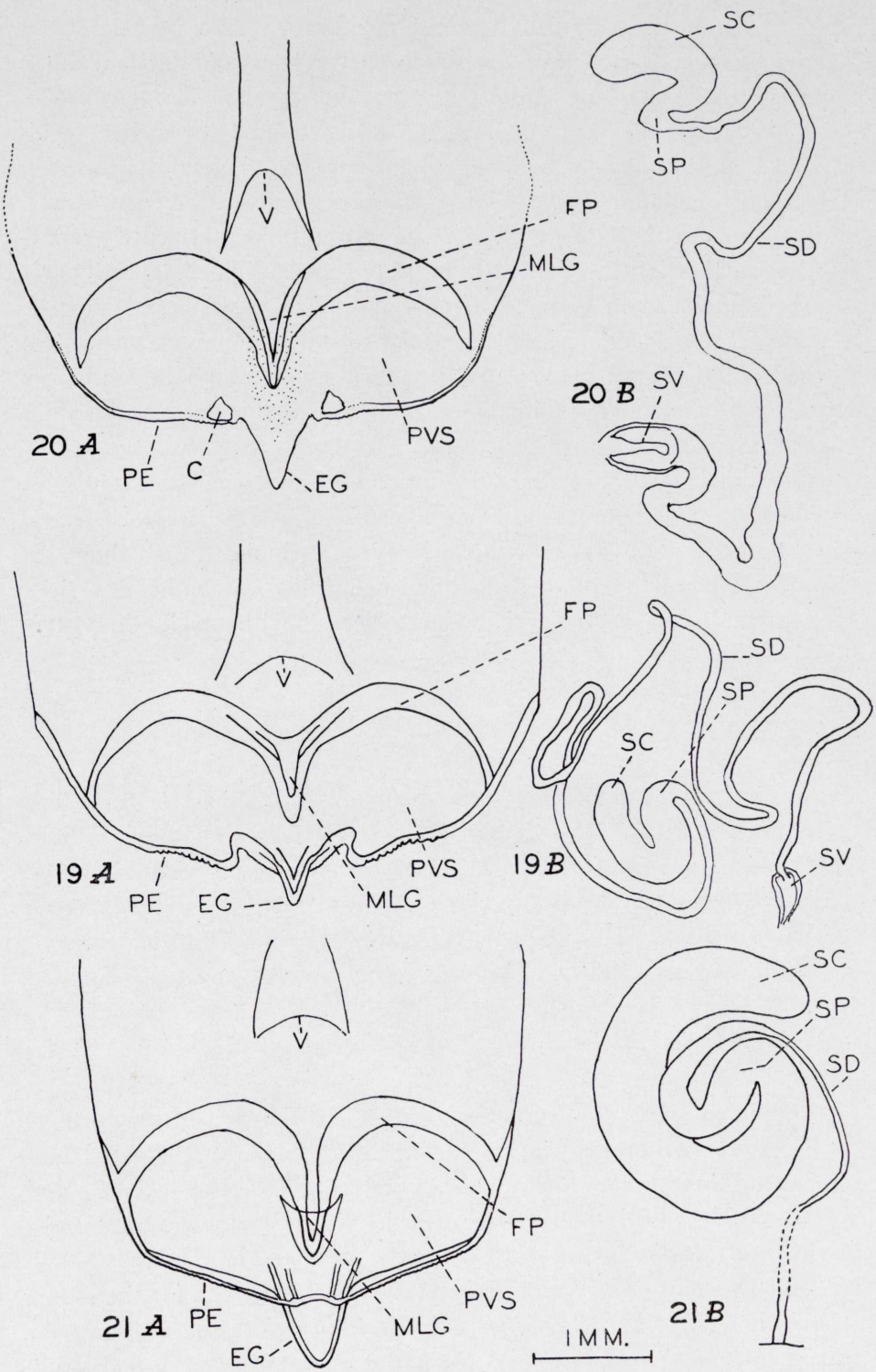
Distribution: Madagascar.

Included genera: Pseudogeloius Dirsh, 1963; *Geloius,* Saussure, 1889.

Species examined: Psedogeloius relictus Dirsh, 1963 (S.S.E. Madagascar — Figs. 17, 19) [Type species]; *P. decorsei* (Bolívar, 1905) [= *P. mahafalensis* Descamps et Wintrebert, 1966] (S.S.W. Madagascar); *P. marolintae* Descamps et Wintrebert, 1966 (Southern Madagascar); *P. fotadrevae* Descamps et Wintrebert, 1966 (C.S. Madagascar); *P. affinis* Kevan, 1965 (S. Madagascar); *Geloius nasutus* Saussure, 1899 (W. and S.W. Madagascar — Figs. 18, 20) [Type species].

Other species: Geloius crassicornis Bolívar, 1905 (? S.W. Madagascar).

Recent accounts of the species included in this tribe are given by Dirsh (1963), Kevan, Akbar and Singh (1964), Kevan (1965), Descamps and Wintrebert (1966 a, b), Dirsh and Descamps (1968) and Kevan (1968 a). Dirsh (1963) figures the phallic structures of *P. relictus,* Kevan (1965) illustrates them for the same species and for *P. affinis,* and Descamps and Wintrebert (1966 b) give figures for their own species as well as for *P. relictus* and *Geloius nasutus* and illustrate the female subgenital armature and spermatheca of *P. decorsei* (as *mahafa-*



Figs. 19-21.—*Geloiini* and *Sagittacridini*, female structures. 19) *Pseudogeloius relictus* Dirsh; 20) *Geloius nasutus* Saussure; 21) *Acanthopyrgus finoti* (Bolívar). *A-B* as in Figs. 4-6. For notation, see pp. 218-220.

lensis), P. fotadrevae and *P. affinis* (as *decorsei).* Kevan (1968 a) illustrates various parts of the phallic structures for all species of *Pseudogeeloius* and for *Geloius nesutus,* as well as the subgenital plate and receptaculum seminis of the last species and of *P. affinis, P. relictus, P. decorsei* (as *mahafalensis)* and *P. fotadrevae.* The spermatheca of *P. relictus* was also illustrated by Dirsh (1963). Dirsh and Descamps (1968) figure genitalic structures (mostly repeated) for *G. nasutus, P. relictus, P. decorsei* (as *mahafalensis), P. fotadrevae* (♂ ♂, ♀ ♀) and *P. marolintae* (♂). A most interesting feature of this tribe is the similary of the male external gemtalia and phallic structures to those of the *Mitricephalini* (Series I, Tribe 5), to which the *Geloiini* may conceivably be distantly related (see above); there are also resemblances in the female structures although these are probably not particularly significant as they are rather generalized. Some members of the present and next tribes bear a fairly strong resemblance to each other.

Tribe 7. Sagittacridini.

(Figs. 21-23).

[Tribus *Pyrgomorphii* (= *Pyrgomorphidae)*], Stirps *Geloius* Saussure, 1899, *Abh. Senckenb. Naturf. Ges.,* XXI, 637 *(partim)* [♂ *Geloius nasutus* = *Acanthopyrgus finoti*].

Subfam. *Geloiinae* Bolívar, 1905, *Bol. Soc. esp. Hist. nat.,* V, 284 *(partim).*

Sect. *Geloii* Bolívar, 1909, *Gen. Ins.,* XC, 4, 50 *(partim);* Johnston, 1956, *Annot. Cat. Afr. Grassh.,* 200 *(partim).*

Geloius Group, Dirsh, 1963, *Bull. Brit. Mus. (nat. Hist.) Ent.,* XIV, 93 *(partim)* [*Geloii,* Strips *(sic) Geloius* and *Geloiinae* all mentioned p. 86 in discussion].

Tribe *Geloiini* Kevan, 1964, *Canad. J. Zool.,* XLII, 436, 437 [*non partim;* although *Geloius* is cited, only *Acanthopyrgus finoti* is referred to]; Kevan, Singh and Akbar, 1964, *Proc. Acad. nat. Sci. Philad.,* CXVI, 232 *(partim)* [*Geloii* and *Geloiinae* also indicated as synonyms]; Kevan and Akbar, 1964, *Canad. Ent.,* XCVI, 1507, 1513, 1524 *(partim)* [*Uhagonia* included]; Kevan, 1966, *Pacif. Ins.,* VIII, 398n.

Tribu *Sagittacr*[*id*]*ini* Descamps and Wintrebert, 1966, *Eos, Madrid,* XLII, 108 *(partim)* [*Uhagonia* included].

Tribe *Sagittacridini* Kevan, *Eos, Madrid, XLIII,* 575, 576, 578.

External features: Body elongate-cylindrical to elongate-fusiform, integument rather smooth, mottled greyish-brown or not; fastigium of vertex long and acute, female antennae not expanded, so far as known;

tegmina and hind wings absent or minute and scale-like; anterior femora of males sometimes spinose below; male terminalia unspecialized.

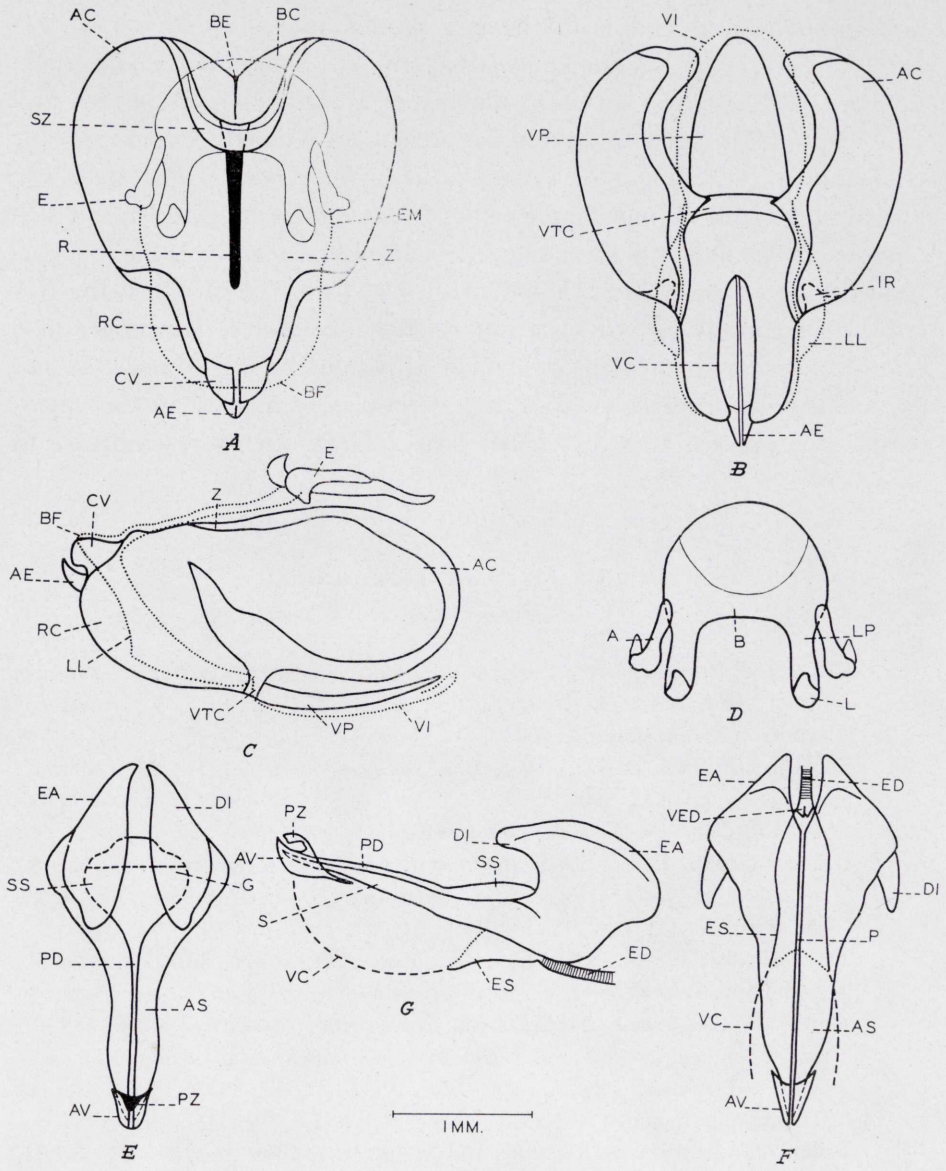


Fig. 22.—*Sagitacridini: Acanthopyrgus finoti* (Bolívar), phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

Principal phallic characters: Epiphallus unspecialized with a narrow bridge and moderate anterior processes, or with the latter large horn-like, and, like the bridge, not well differentiated from the large epiphal-

lic infold lying between them, appendices weak, lophi with dorsally directed apices; ectophallic membrane not forming a hood, central membrane lacking, zygoma very large and covering most of the cingulum and with a median, longitudinal, rod-like thickening, suprazygomal plate small, V-shaped, basal emargination small and shallow, apodemal plates anteriorly rounded in lateral view, valves of cingulum fairly small, triangular, ventral process of cingulum large and tongue-like; aedeagal sclerites undivided apically, rather slender, endophallic apodemes large with large dorsal inflections, posteriorly produced dorsally, ventral anteriorly directed processes absent, spermatophore sac small, round, with an anterior swelling, gonopore before the middle, aedeagal valves very short and obtuse, pseudoarch prominent and posteriorly directed.

Concealed female structures (where known): Subgenital plate with posterior edge somewhat crenulated; egg-guide short and blunt; columellae and contact areas lacking; spermatheca large, S-shaped, the apical part (caecum of spermatheca) very much bigger than the rather poorly differentiated spermathecal vesicle, spermathecal duct comparatively very slender, terminal part without a definite dilation.

Distribution: Madagascar.

Included genera: Acanthopyrgus Descamps et Wintrebert, 1966; *Sagittacris* Dirsh, 1963 (only male known).

Species examined: Acanthopyrgus finoti (Bolívar, 1905) (E. and C. Madagascar — Figs. 21, 22) [Type species]; *A. longicornis* Descapms et Wintrebert, 1966 (N.E. Madagascar); *Sagittacris madagassus* Dirsh, 1963 (N. Madagascar — Fig. 23) [Type species].

Other species: None described.

The most recent accounts of members of this tribe are given by Dirsh (1963), Kevan, Akbar and Singh (1964), Descamps and Wintrebert (1966 a, b), Dirsh and Descamps (1968) and Kevan (1968 a). Dirsh (1953, 1956) figures the epiphallus of *A. finoti* (as *Geloius*); the same author (Dirsh, 1963) gives sketches of the phallic structures and spermatheca of the same species (also as *Geloius*) and of the phallic structures of *Sagittacris madagassus*. Descamps and Wintrebert (1966 b) illustrate the phallic structures of *A. longicornis*, and Dirsh and Descamps (1968) repeat earlier drawings for *A. finoti* (♂, ♀), *A. longicornis* (♂) and *S. madagassus* (♂). Kevan (1968 a) gives preliminary figures of some of the phallic characters of both species of *Acanthopyrgus*. *Sagittacridini* may be related to *Geloiini* as they

are rather similar in appearance although their phallic structures are very different. They may also be related to *Gymnohippini* which have a somewhat similar cingulum; *Uhagonia sphenarioides,* now transferred to the tribe, has certain similarities in external morphology.

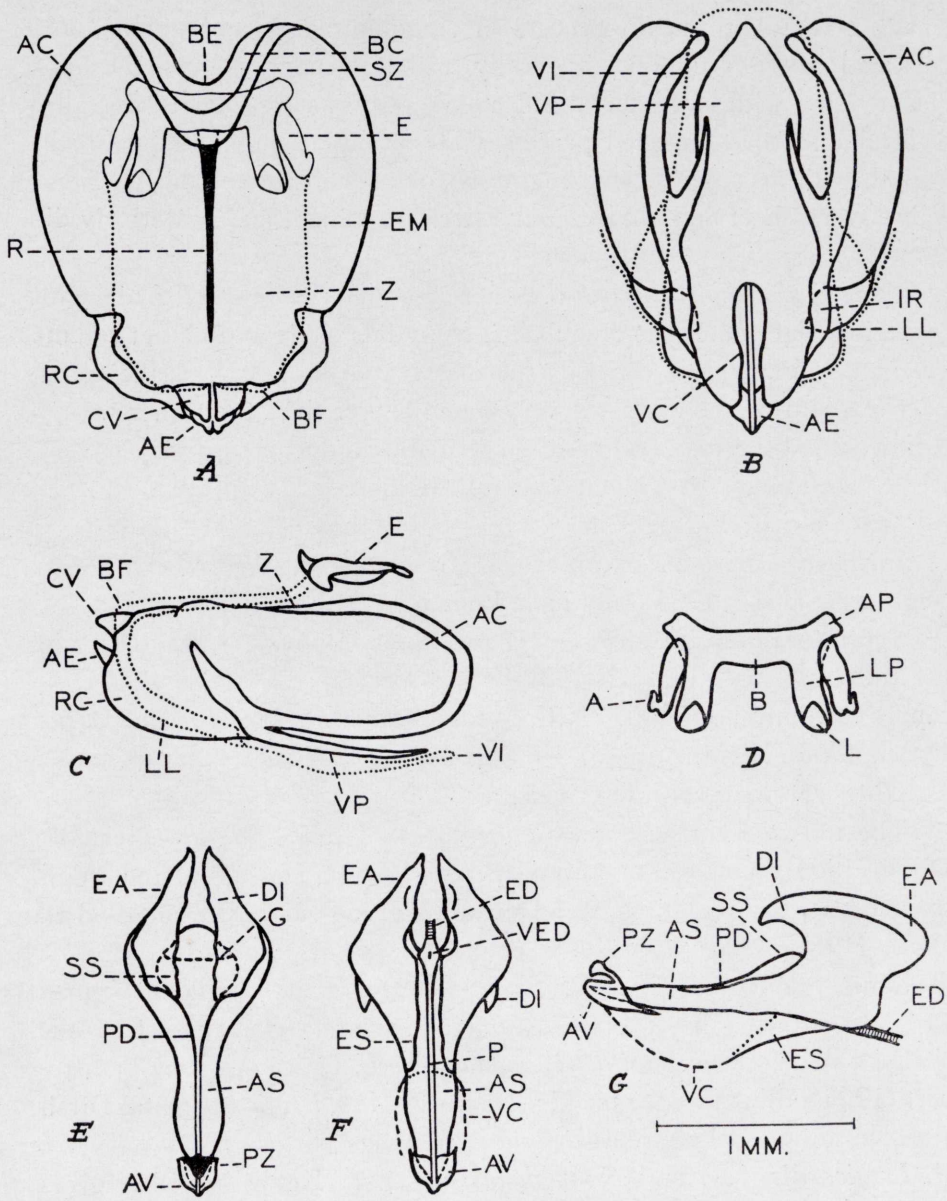


Fig. 23.—*Sagittacridini: Sagittacris madagassus* Dirsh, holotype, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

Tribe 8. Gymnohippini.

(Figs. 14-32, 35-39).

Family *Caloptenidae (Acrididae)* Bruner, 1910, *Voeltzkow Reise Ostafr.*, 1903-1905, II, 636 *(partim)*.

Subfam. *Atractomorphinae* Bolívar, 1905, *Bol. Soc. esp. Hist. nat.*, V, 196 *(partim)* [*Uhagonia*].

Sect. *Atractomorphae* Bolívar, 1909, *Gen. Ins.*, XC, 4, 38 *(partim)*; Johnston, 1956, *Annot. Cat. Afr. Grassh.*, 194 *(partim)* [*Uhagonia*].

Tribe *Atractomorphini* Rehn, 1953, *Grassh. Locusts Austral*, II, 30 *(partim)*; Kevan, 1961, *Ent. mon. Mag.*, XCVI, 204 *(partim)*; Kevan and Banerjee, 1961, *Verh. XI. Int. Kongr. Ent., Wien*, 1960, 23, 24 *(partim)* [*Uhagonia*; p. 24 of last reference suggests removal from tribe].

Fam. *Acrididae* Subfam.] *Catantopinae*, Position Uncertain, Johnston, 1956, *Annot Cat. Afr. Grassh.*, 462 *(partim)* [*Gymnohippus*].

[Fam. *Pyrgomorphidae*], Dirsh, 1961, *Eos, Madrid*, XXXVII, 396 [*Gymnohippus* transferred to].

Tribe *Geloiini* [= *Sagittacridini*], Kevan and Akbar, 1964, *Canad. Ent.*, XCVI, 1507, 1513, 1524 *(partim)* [*Uhagonia*].

Tribe *Gymnohippini* Kevan and Akbar, *Canad. Ent.*, XCVI, 1507, 1513, 1524; Kevan, 1966, *Pacif. Ins.*, VIII, 398 [transfer of *Uhagonia*]; Descamps and Wintrebert, 1966, *Bull. Soc. ent. Fr.*, LXXI, 26, 1966, *Eos, Madrid*, XLII, 101; Kevan, 1968, Ibid., XLIII, 575, 578.

Tribu *Sagittacr*[*id*]*ini* Descamps and Wintrebert, 1966, *Eos, Madrid*, XLII, 108 *(partim)* [*Uhagonia*].

External features: Body fusiform or short and robustly cylindrical, integument rather evenly granular, usually greenish, or pale brownish; fastigium of vertex acute, triangular to short and blunt, if latter, frontal costa below fastigium more or less vertical for a short distance and not distinctly excised in profile; female antennae not expanded; tegmina and hind wings absent or greatly reduced; male abdominal terminalia unspecialized except sometimes for elongate cerci.

Principal phallic structures (where known); Epiphallus unspecialized with small anterior processes and narrow or moderately narrow bridge, appendices rather small or of moderate size, lophi with dorsally or dorsolaterally directed apices; ectophallic membrane not very extensive, unspecialized, central membrane lacking, zygoma covering most of the cingulum and usually with a variably developed, median, rod-like thickening with a pair of transverse arms, suprazygomal plate varying from large and rectangular to small and insignificant or even lacking, basal emargination very shallow, apodemal plates more or less rounded

anteriorly in lateral view, without ventral processes, valves of cingulum small to insignificant, lobe-like, ventral process of cingulum lacking; aedeagal sclerites undivided apically, fairly to very short and rather

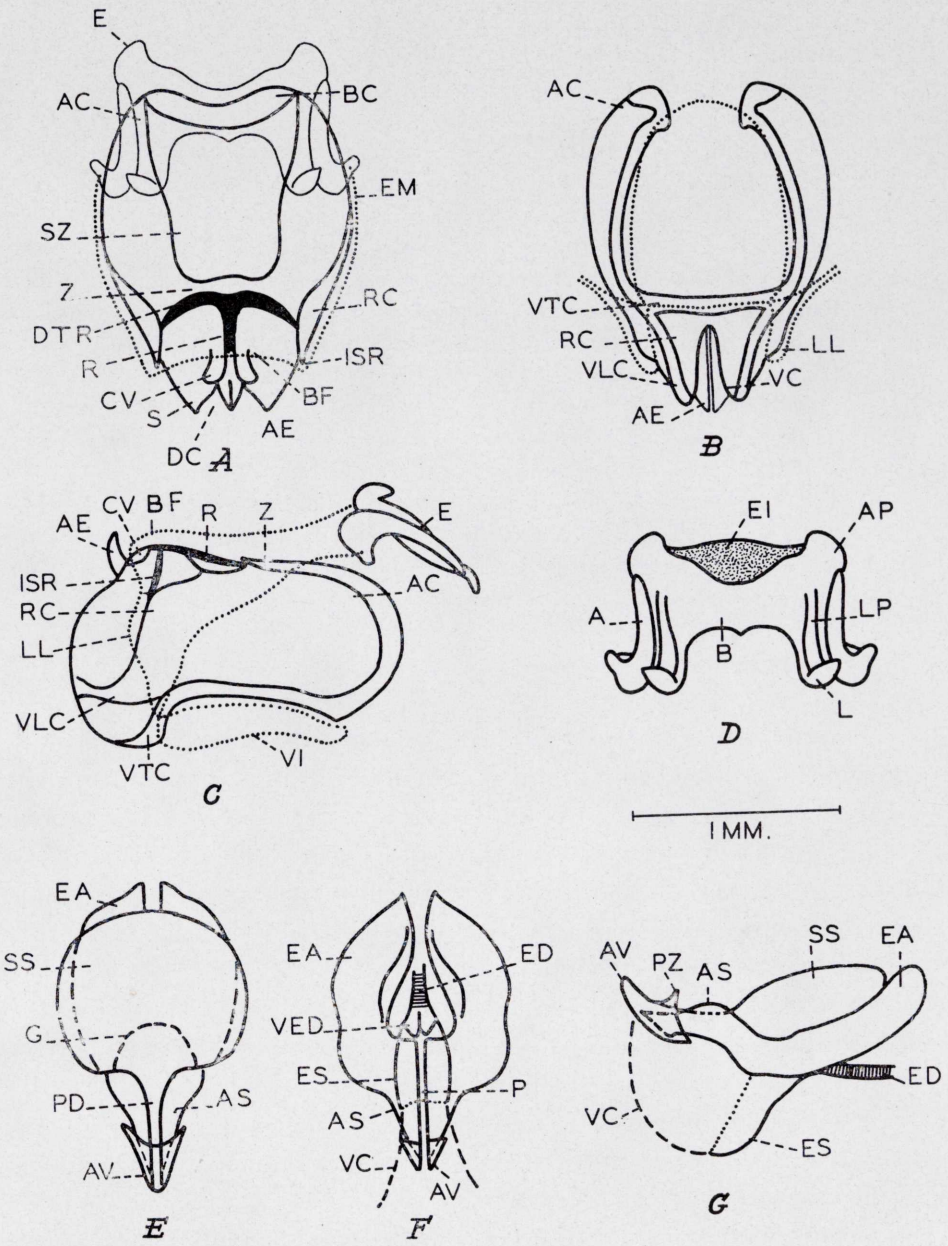


Fig. 24.—*Gymnohippini: Pyrgohippus pallidus* Dirsh, paratype, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

stout, rather unusual in profile, endophallic apodemes partially or almost completely dorsoventrally flattened to form rather wing-like ex-

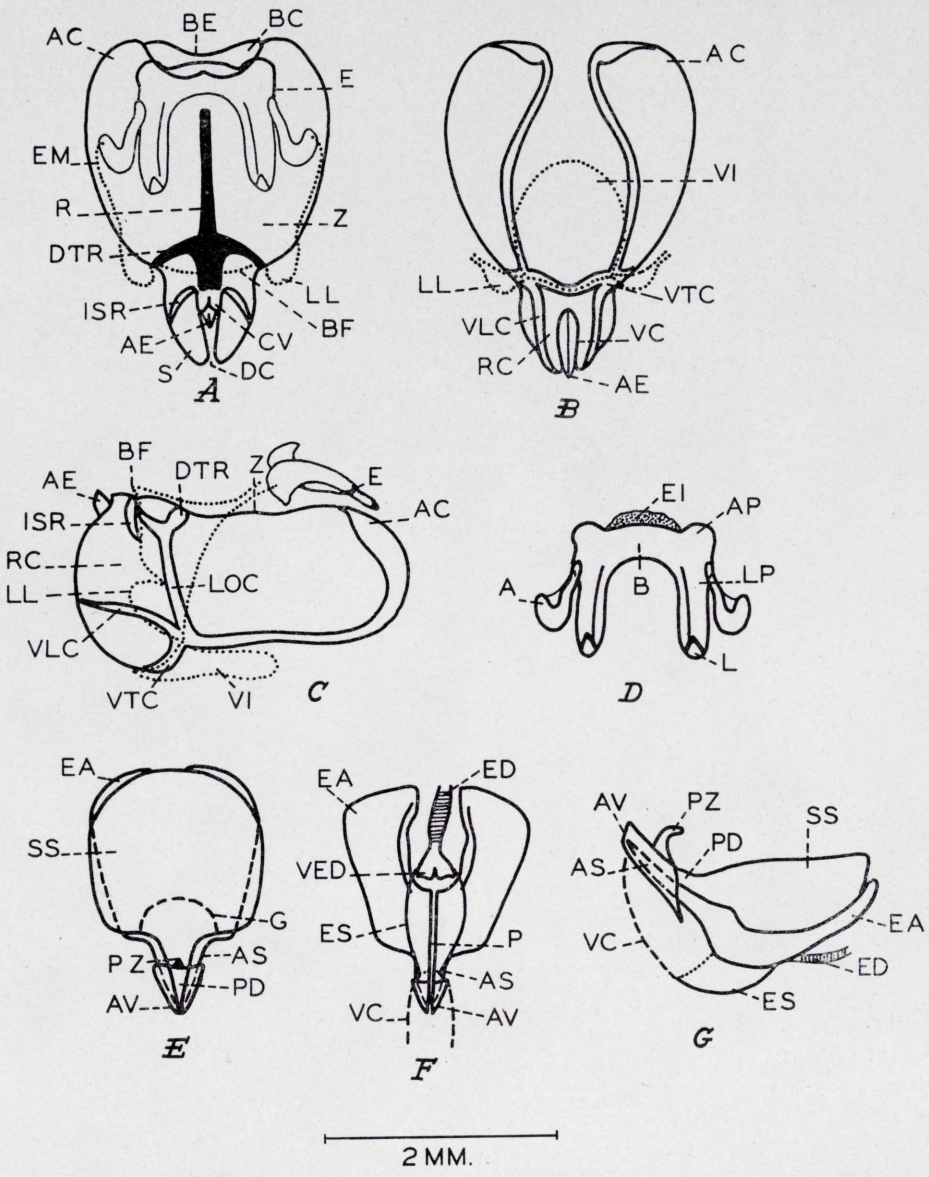
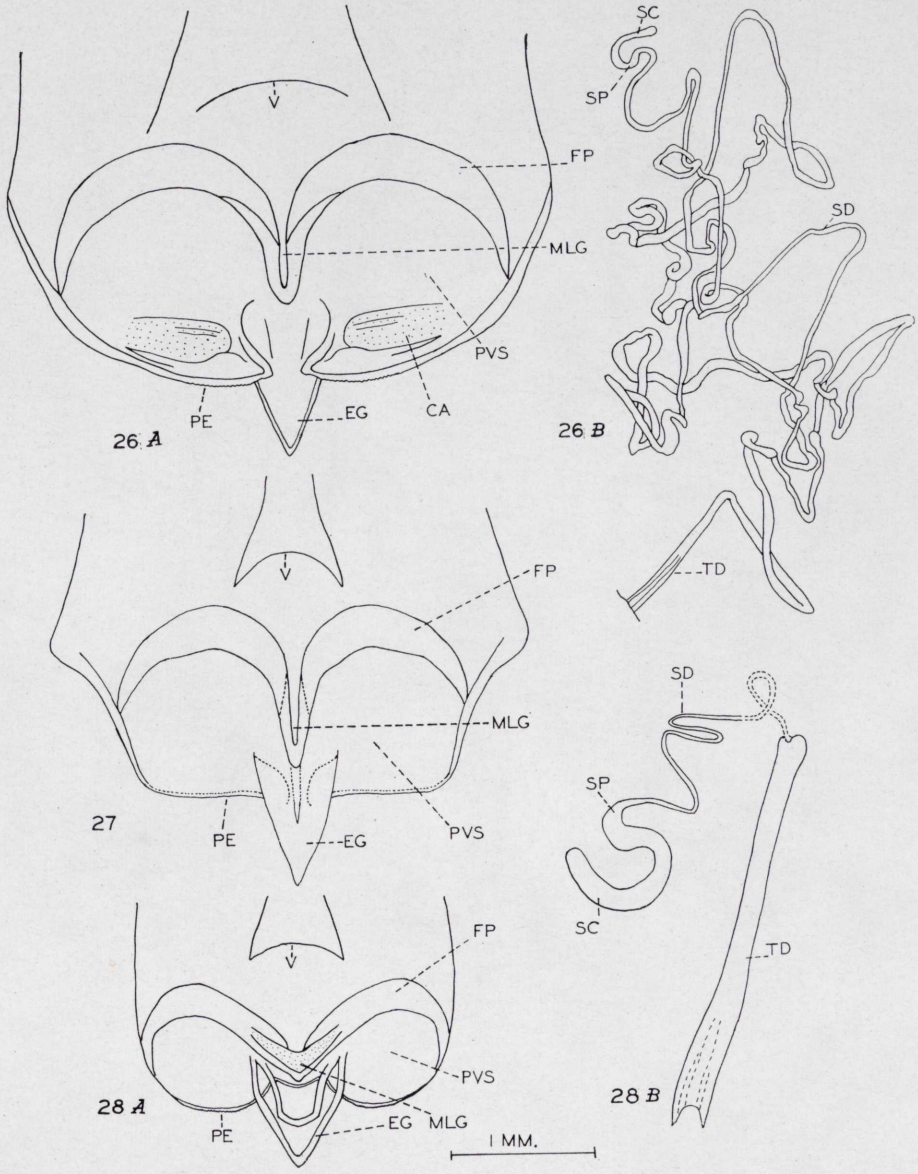


Fig. 25.—*Gymnohippini: Gymnohippus marmoratus* Bruner, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

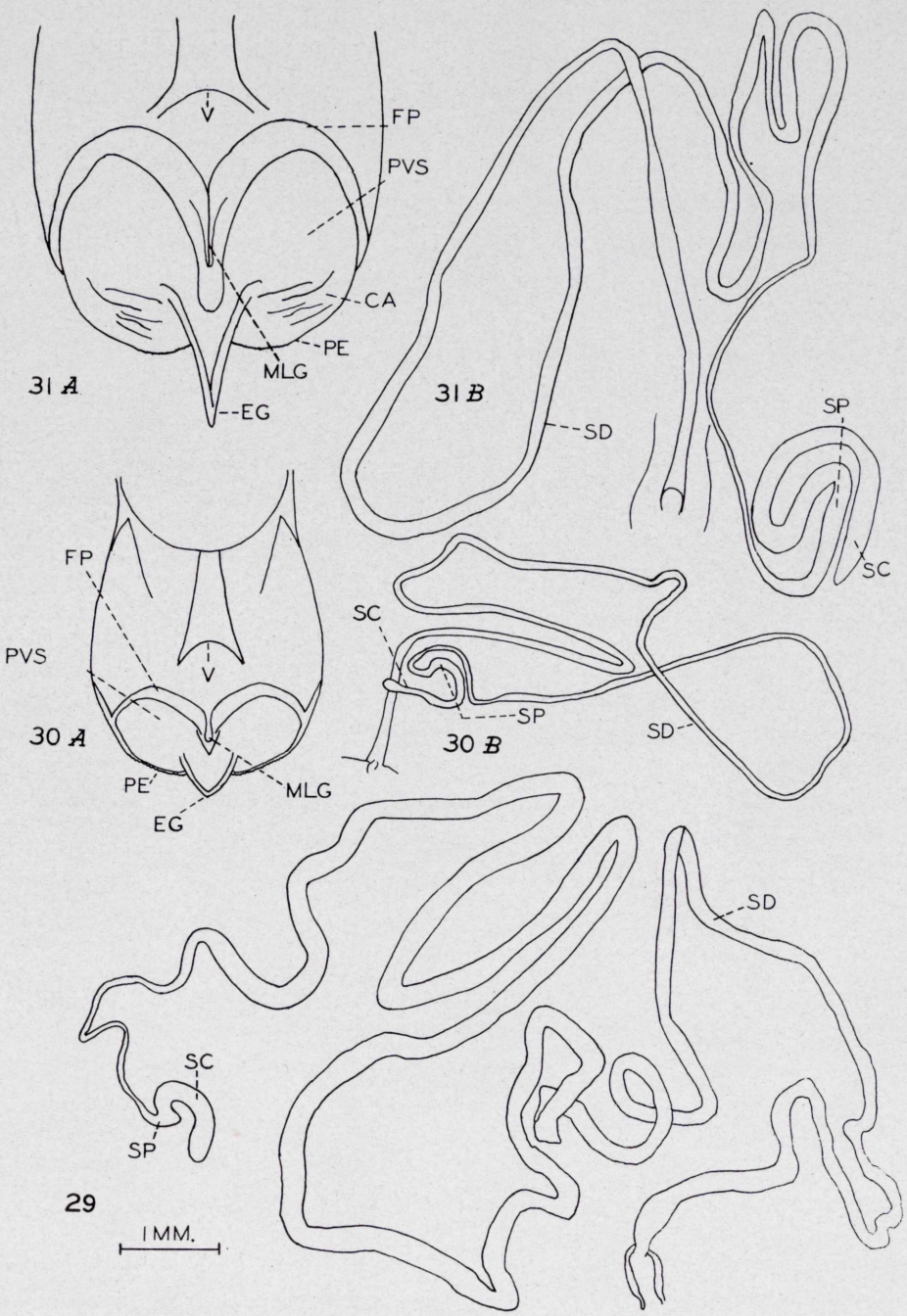
pansions, without dorsal inflections or ventral processes, spermatophore sac very large, round or oval, covering almost all the rest of the endophallus, extending on either side up to or beyond the bases of the

aedeagal sclerites and the endophallic apodemes, gonopore very distinctly posterior in position, aedeagal valves very short and triangular; pseudoarch very small.

Concealed female structures: Subgenital plate with posterior edge



Figs. 26-28.—*Gymnohippini,* female structures. 26) *Uhagonia depressa* Dirsh, holotype *(A,* subgenital plate, dorsal; *B,* receptaculum seminis); 27) *Pyrgohippus productus* (Descamps et Wintrebert), subgenital plate, dorsal (for receptaculum seminis, see Fig. 29); 28) *Gymnohippus marmoratus* Bruner *(A,* subgenital plate, dorsal; *B,* receptaculum seminis). For notation, see pp. 218-220.



Figs. 29-31.—*Gymnohippini,* female structures. 29) *Pyrgohippus productus* (Descamps et Wintrebert), receptaculum seminis (for subgenital plate, see Fig. 27); 30) *Pyrgohippus pallidus* Dirsh, paratype *(A,* subgenital plate, dorsal; *B,* receptaculum seminis); 31) *Uhagonia sphenarioides* Bolívar, holotype *(A,* subgenital plate, dorsal; *B,* receptaculum seminis). For notation, see pp. 218-220.

crenulated; egg-guide broadly triangular; columellae absent; indications of contact areas sometimes present; spermatheca of a simple, open 'S' shape, sometimes little wider than the spermathecal duct, the caecum undifferentiated from the spermathecal vesicle, spermathecal duct usually very long, terminal part distinctly wider than the rest of the duct, but without a dilation.

Distribution: Madagascar.

Included genera: Uhagonia Bolívar, 1905; *Pyrgohippus* Dirsh, 1963; *Gymnohippus* Bruner, 1910.

Species examined: Uhagonia sphenarioides Bolívar, 1905 (C. Madagascar [8] — Fig. 31) [Type species]; *U. depressa* Dirsh, 1963 (N.E. Madagascar — Fig. 26); *U. wintreberti* Kevan, 1968 (N.E. Madagascar — Figs. 35-39, Pl. I — see Appendix); *Pyrgohippus pallidus* Dirsh, 1963 (S.W. Madagascar — Figs. 24, 30) [Type species]; *P. productus* (Descamps et Wintrebert, 1966) (S. C. Madagascar — Figs. 27, 29, 32); *Gymnohippus marmoratus* Bruner, 1910 (S.W. Madagascar — Figs. 25, 28) [Type species].

Other species: None known.

This tribe is made up of genera that were not originally associated with one another. All but the most recently described species are treated by Dirsh (1963), who gives sketches of the phallic structures and spermathecae of *Pyrgohippus pallidus* and *Gymnohippus marmoratus*. *Gymnohippus* was revised by Kevan (1963 b). The same author (Kevan, 1968 a) refers briefly to the various genera, transferring *productus* from *Gymnohippus* to *Pyrgohippus*. Descamps and Wintrebert (1966 b) illustrate both phallic and female structures of *Pyrgohippus productus* (as *Gymnohippus)*. Dirsh and Descamps (1968) repeat earlier genitalic figures for *G. marmoratus, G. productus* and *P. pallidus* (♂♂, ♀♀); they also give others for *U. wintreberti*. Tribal relationships seem to be on the one hand with the *Sagittacridini* (see above), and on the other with *Malagasphenini* (further).

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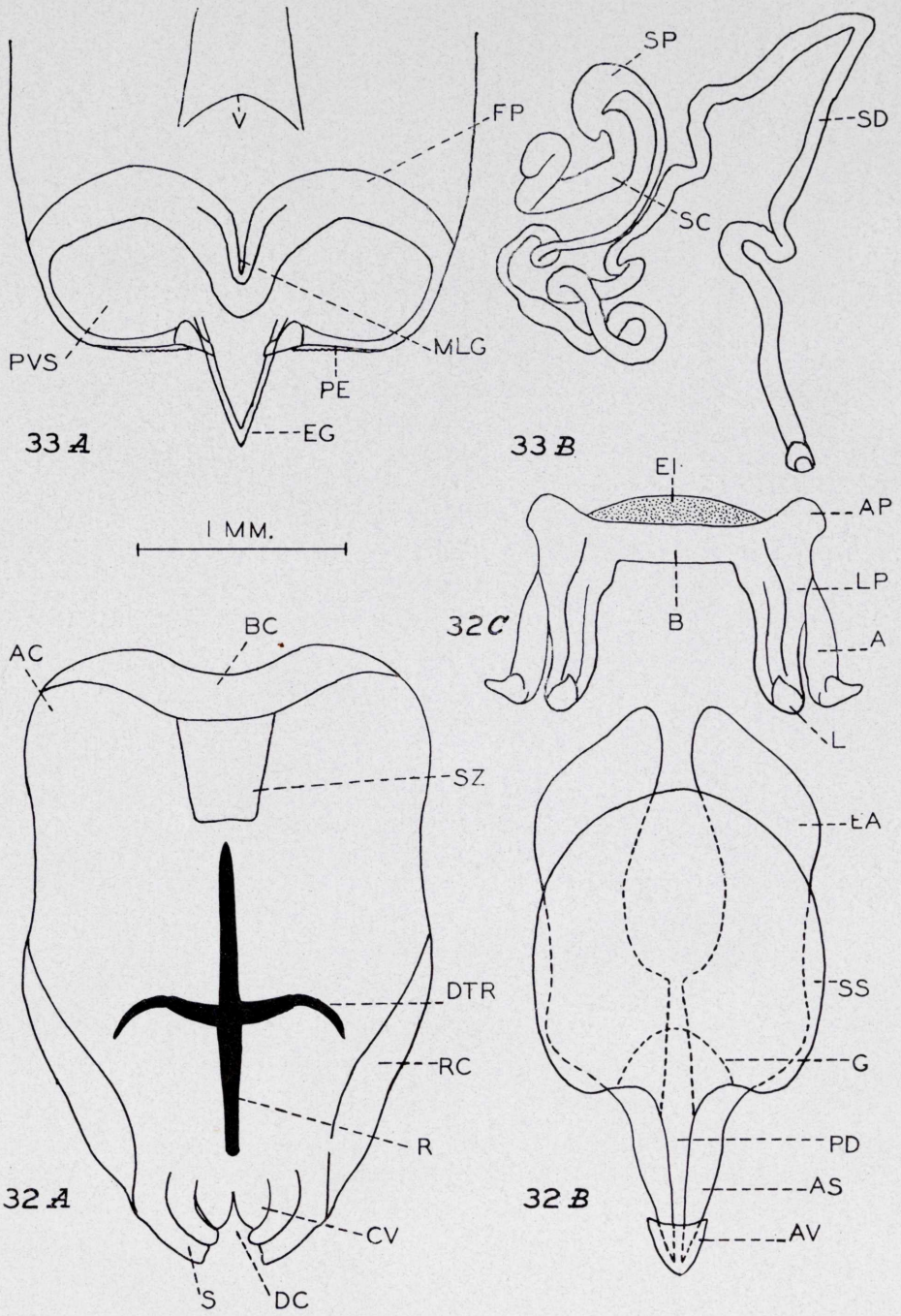
[8] Only the female holotype is known. It bears the followings labels: (1) 18794 [Brunner von Wattenwyl's number], (2) 35 [on pink], (3) *Uhagonia sphenarioides* Bol., Bol. det. [in Brunner's, not Bolívar's, hand]. There is no locality label on the specimen, but the cabinet label indicates "Central-Madagascar".



Figs. 32-33.—*Gymnohippini* and *Malagasphenini*. 32) *Pyrgohippus productus* (Descamps et Wintrebert), phallic structures (*A*, ectophallus, dorsal; *B*, endophallus, dorsal; *C*, epiphallus, dorsal); 33) *Malagasphena minor* Kevan, Akbar and Singh, female structures (*A*, subgenital plate, dorsal; *B*, receptaculum seminis). For notation, see pp. 218-220.

Tribe 9. Malagasphenini.

(Figs. 33, 34).

Tribe *Orthacridini* Kevan, Akbar and Singh, 1964. *Trans. Amer. ent. Soc.*, XC, 112 *(partim)*.

Tribe *Malagasphenini* Kevan and Akbar, 1964, *Canad. Ent.*, XCVI, 1507, 1513, 1524.

External features: Body rather cylindrical but not elongate, integument punctured, not evenly granular, usually beset with a few widely spaced pustules; fastigium of vertex rather short and acute, antennae cylindrical; tegmina and hind wings reduced to minute scales; male terminalia unspecialized.

Principal phallic characters: Epiphallus with a very narrow bridge and long, narrow lateral plates, anterior projections poorly developed, somewhat rounded, appendices of moderate size, lophi strong with more or less dorsally directed apices; ectophallic membrane not extensive, extending much beyond the middle of the cingulum, central membrane small and rather broad, zygoma large extending over he basal half of the cingulum, without a median, rod-like thickening, broadly excised posteriorly, suprazygomal plate fairly small, elongate-rectangular, basal emargination small but distinct, apodemal plates rather narrowly rounded anteriorly in lateral view, without ventral processes, valves of cingulum rather small and lobe-like, ventral process of cingulum broadly parabolic; aedeagal sclerites undivided apically, rather short and broad, endophallic apodemes somewhat dorsoventrally flattened and with small dorsal inflections, ventral processes absent, spermathophore sac comparatively very large, elongate-oval, but not extending laterally beyond the margins of the aedeagal sclerites or endophallic apodemes, gonopore very distinctly posterior in position, aedeagal valves short and rather triangular, pseudoarch small.

Concealed female structures: Subgenital plate with posterior edge slightly serrated and egg-guide triangular and prominent; columella-like structures poorly developed immediately to either side of the base of the egg-guide, contact areas absent. Spermatheca distinctly divisible into vesicle and caecum, the former having a distinct apical pocket not found in other tribes of Series II, spermathecal caecum somewhat convoluted, spermathecal duct rather thick, terminal part not distinctly widened, terminal dilation lacking.

Distribution: Madagascar.

Included genus: Malagasphena Kevan, Akbar and Singh, 1964.

Species examined: Malagasphena minor Kevan, Akbar and Singh, 1964 (E. Madagascar — Figs. 33, 34) [Type species].

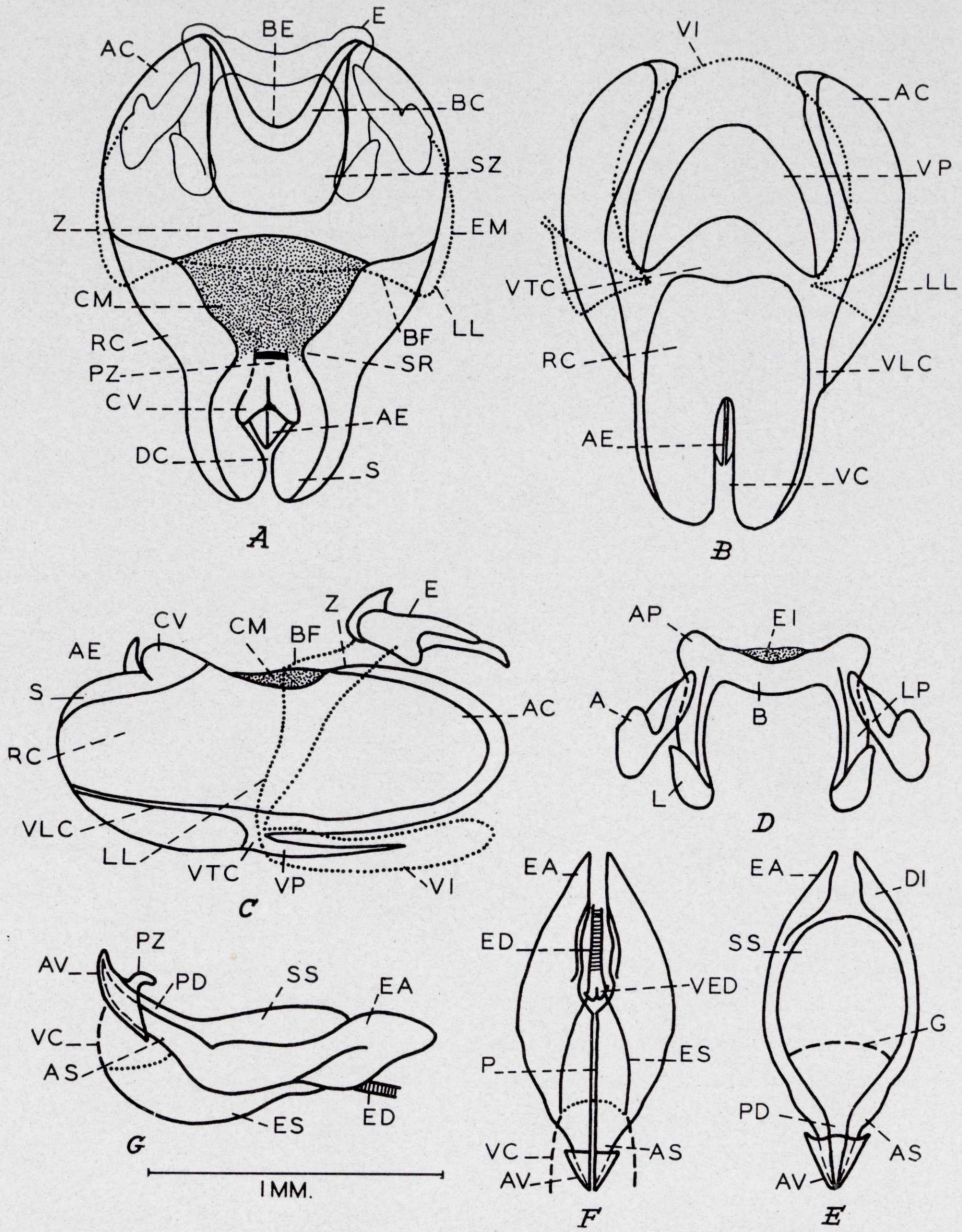


Fig. 34.—*Malagasphenini: Malagasphena minor* Kevan, Akbar and Singh, phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

Other species: None known.

Kevan, Akbar and Singh (1964) give preliminary figures of the phallic strucures of the type species. This tribe is similar to the last in several features of external morphology, in the general form of the cingulum (except that the zygoma is short and there is a distinct, if small, central membrane and a ventral process), in the dorso-ventrally (though less) flattened endophallic apodemes and in the large (although more elongate and less wide) spermatophore sac. The phallic structures are, in fact, less specialized than in *Gymnohippini* (and other tribes of Series II). The concealed female structures also show more primitive characters, notably the presence of columella-like structures at the base of the egg-guide, the apical pocket of the spermathecal vesicle and the short, convoluted spermathecal caecum. Certain affinities with *Orthacridini* and *Popoviini* (Series III) seem to be indicated.

List of Abbreviations.

The following is a list, arranged alphabetically, of the abbreviations used in the illustrations.

A, Appendix of epiphallus.
AB, Apical bulb of spermathecal appendage.
AC, Apodemal plate of cingulum.
AE, Aedeagus.
AP, Anterior projection of epiphallus.
AS, Aedeagal sclerite.
AS_1, The basal part of AS when separated from the apical part.
AS_2, The apical part of AS when separated from the basal part.
AV, Aedeagal valve.
B, Bridge of epiphallus.
BC, Basal thickening of cingulum.
BE, Basal emargination of cingulum.
BF, Basal fold of ectophallic membrane.
C, Columella of female subgenital armature.
CA, Contact area of female subgenital armature.
CM, Central membrane of ectophallus.
CV, Valve of cingulum.
DC, Dorsal cleft of cingulum.
DI, Dorsal inflection of endophallic apodeme.

DTR, Dorsal transverse ridge of cingulum.
E, Epiphallus.
EA, Endophallic apodeme.
ED, Ejaculatory duct.
EG, Egg-guide.
EI, Epiphallic infold.
EM, Ectophallic membrane.
ES, Ejaculatory sac.
FP, Floor pouch of female genital chamber.
G, Gonopore (male).
H, Hood of ectophallus.
IR, An internal inflected process on the ramus of the cingulum.
ISR, Inflection of ramus or supraramus.
L, Lophus of epiphallus.
LL, Lateral lobe of ectophallic membrane.
LOC, Lateral oblique thickening of cingulum.
LP, Lateral plate of epiphallus.
MLG, Median longitudinal groove of ovitract.
O, Orifice of spermathecal duct.
P, Phallotreme.
PD, Phallotreme duct.
PE, Posterior edge of female subgenital plate.
PVS, Post-vaginal sclerite of female genital chamber.
PZ, Pseudoarch of ectophallus.
PZI, Posterior inflection of cingulum.
R, A longitudinal, mid-dorsal ridge of the cingulum.
RC, Ramus of cingulum.
RP, A specialized process arising from RC.
S, Sheath of ectophallus.
SA, Spermathecal appendage; the 'apical diverticulum' and homologous diverticula of previous authors.
SB, Secondary diverticulum of caecum of spermatheca or occasionally of spermathecal vesicle.
SC, Caecum of spermatheca; with (part of) the spermathecal vesicle is the 'preapical diverticulum' of previous authors.
SD, Spermathecal duct.
SL, Secondary diverticulum of spermathecal appendage (or occasionally of spermathecal duct).
SP, Spermathecal vesicle.

SR, Supraramus of cingulum.
SS, Spermatophore sac.
V, Valve of spermathecal duct.
SZ, Suprazygomal plate of cingulum.
TD, Terminal dilation of spermathecal duct.
V, Vulva, or Opening of vagina, or Common oviduct, or Female gonopore.
VAC, Ventral process of apodemal plate of cingulum.
VAV, A ventral process on the aedeagal valve.
VC, Ventral cleft of cingulum.
VEA, Ventral process of endophallic apodeme.
VED, Valve of ejaculatory duct.
VI, Ventral infold of ectophallic membrane.
VLC, Ventral longitudinal thickening of cingulum.
VP, Ventral process of cingulum.
VTC, Ventral transverse thickening of cingulum.
Z, Zygoma of cingulum.

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APPENDIX.

ON *Uhagonia wintreberti*.

BY

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The Malagasy genus *Uhagonia* Bolívar, 1905, was formerly known only by two unique females: the respective holotypes of *U. sphenarioides* Bolívar, 1905, and *U. depressa* Dirsh, 1963, the former from an unspecified locality (C. Madagascar according to the cabinet label with the specimen in the Vienna Museum), and the other from 1700 m. in the Marojeje Massif in the eastern part of northern Madagascar.

Through the kindness of M. M. Descamps of the Paris Museum, I have now been able to examine a series of *Uhagonia*, including ma-

les, from another mountainous region, the Tsaratanana Massif in central northern Madagascar. This region is in the same general area as the type locality of *U. depressa,* but is separated from it by somewhat lower terrain. The female specimens in question resemble the holotype of *U. depressa,* but differ in being a little less stout *(U. sphenarioides* is more elongate), in having a longer fastigium of the vertex (although not nearly so long as in *U. sphenarioides),* distinct, though minute tegminal vestiges *(U. depressa* is subapterous, although not strictly devoid of all traces of wings; *U. sphenarioides* has somewhat larger tegminal scales), and an even longer and more slender ovipositor *(U. sphenarioides* is not unlike *U. depressa).* The female subgenital plate and spermatheca are intermediate in form between those of the two previously described species.

Uhagonia wintreberti Kevan *in* Dirsh & Descamps, 1968[9].
(Figs. 35-39; Pl. I).

'Holotype'[10] ♂ : Madagascar Nord, Mt. Tsarantanana, 1500-2500 m; 5 au 10-XI-1960, TS. 320 (D. Wintrebert rec.) [Muséum National d'Histoire Naturelle, Paris].

Much smaller than the female; integument evenly granular. *Antennae:* shorter than head and pronotum together, triquetrous, of even thickness almost throughout. *Head* (fig. 37): fastigium of vertex acute, a little longer than wide, about equal in length to the longest diameter of an eye; frontal ridge strongly excised in profile just below fastigium of vertex; cheeks with a few low callous tubercles behind and below the eyes. *Thorax:* pronotum (fig. 37) divergent behind, but less so than in female, anterior margin subtruncate, posterior margin excised, median transverse sulcus crossing the disc about the middle,

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[9] Dirsh and Descamps (1968), p. 93, fig. 41, p. 94) refer to, and illustrate the genitalic structures of '*Uhagonia* sp.', but they also (p. 94, footnote) published the combination *U. wintreberti* Kevan in anticipation of the present description (unavoidably delayed). Their figures, etc., however, technically constitute a 'description' for the purposes of nomenclature, so that the species dates from 1968 and not from the present work. As they did not directly attach the specific name to the figures, etc., it would seem that the above method of citation is the most appropriate.

[10] In view of the premature 'description', this should perhaps more properly regarded as the lectotype.

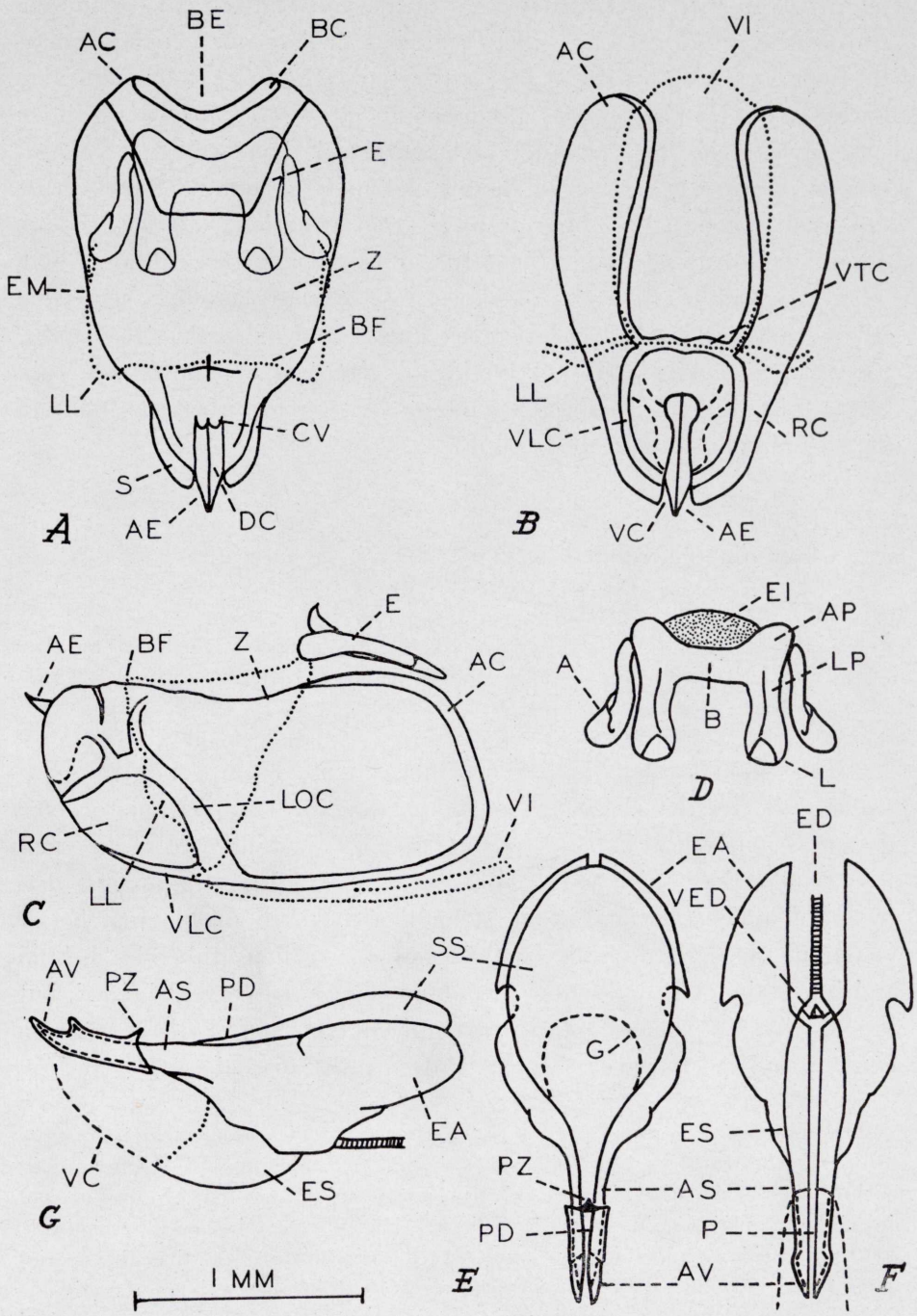

Fig. 35.—*Gymnohippini: Uhagonia wintreberti* Kevan, 'paratypes' phallic structures. *A-G* as in Fig. 1. For notation, see pp. 218-220.

typical sulcus slightly arcuate at about midway between the median sulcus and the posterior margin, lateral pronotal lobes with anterior margin straight, oblique, posterior margin almost vertical, slightly excavate, inferior margin rather straight, infero-posterior angle slightly less than a right-angle; mesonotum shorter, metanotum slightly longer than the metazona of the pronotum; prosternal tubercle transverse, flattened, truncated apically; mesosternal lobes subquadrate, their interspace about one-and-a-half times the width of a lobe; metasternal pits open, somewhat closer together than the inner posterior angles of the mesosternal lobes, connected posteriorly by a curved, transverse suture. *Wings:* tegminal vestiges minute, ovate, rounded apically, narrow at their bases, just surpassing the posterior margin of the mesonotum. *Legs:* hind femur stout, considerably surpassing abdomen, strongly keeled on outer face. *Abdomen:* tympana lacking; epiproct broadly triangular, about as wide as long, cerci conical, not surpassing epiproct; subgenital plate somewhat compressed, truncated apically in lateral view, pointed in dorsal view; phallic structures (from a 'paratype') [11] as illustrated (fig. 35).

Coloration: generally olive green, abdomen yellowish ventrally; antennae blackish above; eyes brown; pronotal disc with a shiny yellow macula on either side of the posterior margin in front of the tegminal vestiges; latter blackish with a central greenish-yellow spot; hind femora yellowish green; hind tibiae green in the basal third, crimson in the apical two-thirds; hind tarsi crimson.

Measurements: length (apex of fastigium to tip of abdomen) 13, pronotum 3.2, tegmen 0.5, hind femur 8.0 mm.

'*Allotype*' [12] ♀ : same data as 'holotype' [Paris]. Very similar to *U. depressa,* but differing as already noticed; agreeing with the above description of the male in its essential features, but much larger and more robust (fig. 38), differing principally as follows: inferior margin of lateral pronotal lobe with a few small granular tubercles anteriorly; mesonotum very short, virtually concealed; interspace between mesosternal lobes about twice as wide as a lobe; metasternal pits widely spaced, about as far apart as the inner posterior angles of the mesosternal lobes; tegminal vestiges reaching almost half-way along the meta-

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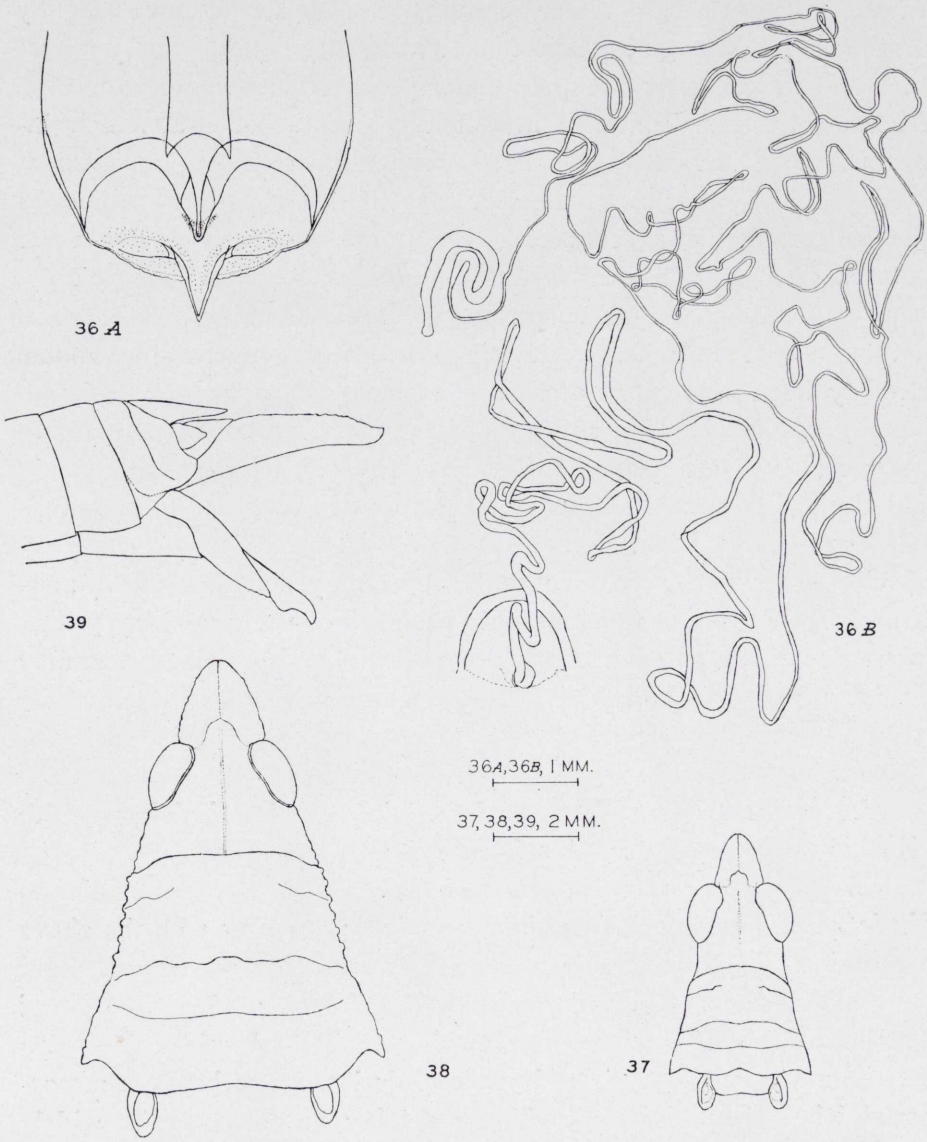
[11] Possibly more correctly to be regarded as a paralectotype (see Footnote 10).

[12] Possibly more correctly to be regarded as a 'lectallotype' (see Footnote 10).

notum; hind femora not surpassing the end of the abdomen; cerci much shorter than epiproct. Ovipositor, subgenital plate and spermatheca (from a 'paratype') as illustrated (figs. 36, 39).



Figs. 36-39.—*Gymnohippini: Uhagonia wintreberti* Kevan, 'paratypes'. 36) female structure (*A*, subgenital plate, dorsal; *B*, spermatheca; for notation, see pp. 218-220; 37) head and pronotum, ♂, dorsal; 38) *id.*, ♀; 39) ovipositor, lateral.

Coloration: generally as in 'holotype', but differing as follows: small tubercles on cheeks and lateral pronotal lobes yellowish green; yellow maculae lacking on the posterior margin of the pronotal disc; cheeks

and lateral pronotal lobes with a few blackish marks; pattern on outer face of hind femur filled in with blackish; hind tarsi green.

Measurements: length 28.5, pronotum 5.2, tegmen 0.8, hind femur 12.3 mm.

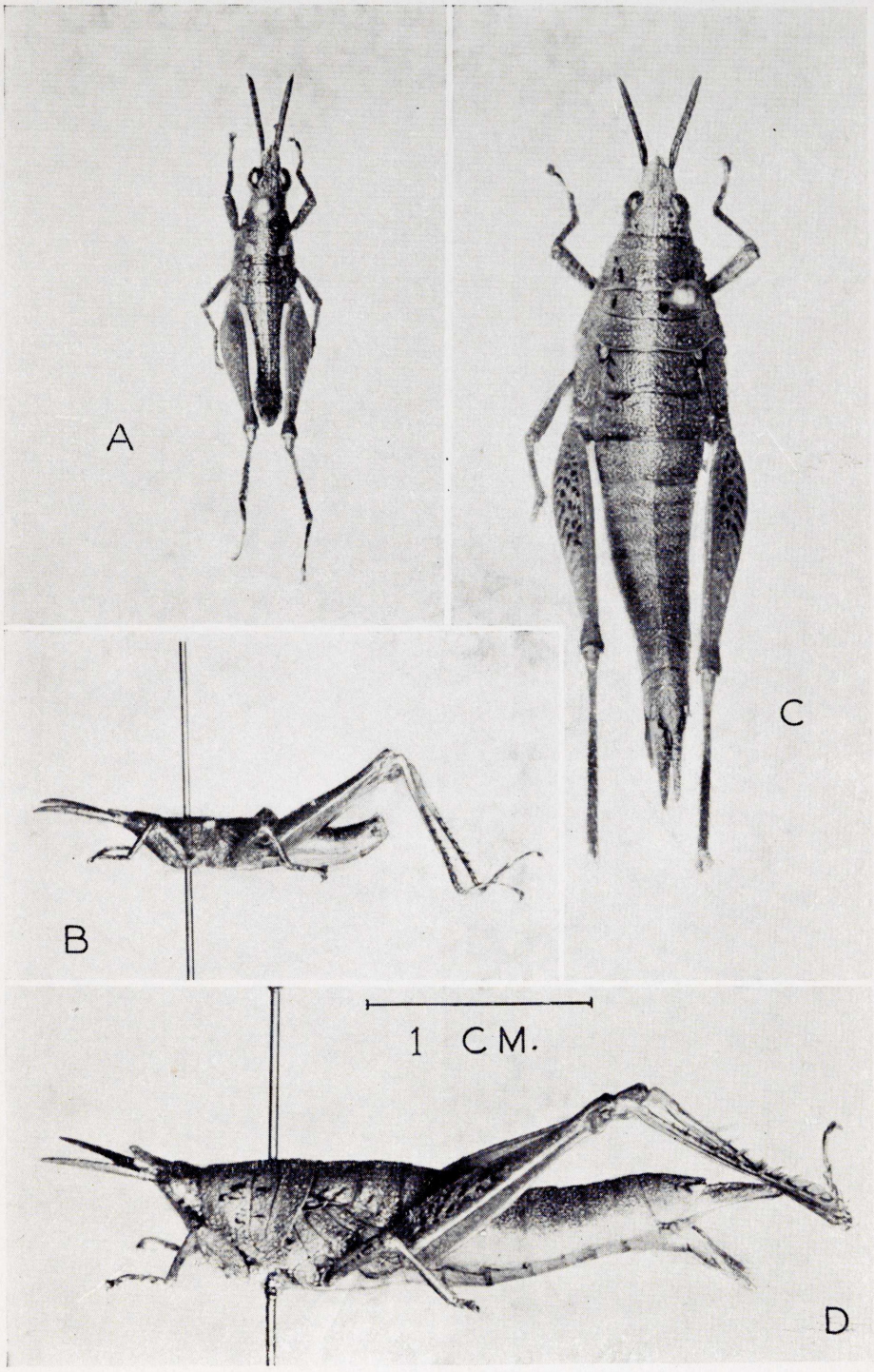
'Paratypes': 15 ♂♂, 16 ♀♀, same data as 'holotype'. The series also contains 10 juveniles.

The 'paratypes' vary considerably in size, but the males are all very much smaller than the females. There are also minor variations in colour, but the yellow maculae on the pronotum seem to be characteristic of the male. One female is basically reddish brown instead of olive green.

The species is dedicated to Dr. D. Wintrebert who has added greatly to our knowledge of Madagascar Orthoptera.

EXPLANATION OF PLATE III:

Uhagonia wintreberti Kevan. A) 'holotype' ♂, dorsal; B) *id.*, lateral; C) 'allotype', dorsal; D) *id.*, lateral.



D. KEITH MCE. KEVAN, SEYD S. AKBAR and YU-CHEN CHANG: The concealed copulatory structures of the *Pyrgomorphidae (Orth. Acridoidea)*.